DIADECTES (DIADECTOMORPHA: DIADECTIDAE) FROM THE EARLY PERMIAN OF CENTRAL GERMANY, WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT

A new species of the diadectomorph *Diadectes*, *D. absitus*, is described on the basis of a nearly complete, articulated skeleton that includes the skull, an isolated skull, and the greater portions of two articulated postcrania. All were collected from fluvial red-bed deposits immediately above the Tambach Sandstone, middle part of the Lower Permian Tambach Formation, lowermost formational unit of the Upper Rotliegend, of the Bromacker locality in the midregion of the Thuringian Forest near Gotha, central Germany. *Diadectes absitus* represents the first member of this genus to be described from outside of North America. A combination of autapomorphic and plesiomorphic characters provides a more substantial basis for recognizing *D. absitus* than is available for distinguishing between the North American species of *Diadectes*. Two possible conclusions are drawn from the relationship of *D. absitus* to the North American members of the genus: 1) its uniqueness reflects the wide geographic separation from the North American species, and 2) its greater primitiveness reinforces previous assessments of the biostratigraphic position and age of the Tambach Formation as earliest Permian Wolfcampian.

KEY WORDS: Diadectidae (*Diadectes*), Upper Rotliegend, skeleton, Bromacker locality, Germany, Pangaea

INTRODUCTION

Until very recently, the presence of diadectids in the Lower Permian of Europe has been limited to two very incomplete specimens described over a century ago from the Lower Rotliegend of Germany. A string of four presacrals and two sacrals from the Leukersdorf Formation of the Erzgebirge Basin near Zwickau was described by Meyer (1860) as *Phanerosaurus naumanni*, and Geinitz and Deichmueller (1882) described *P. pugnax* on the basis of disarticulated skull and postcranial elements from the Niederhaeslich in the Doehlen Basin near Dresden. In a lengthy restudy of the latter species, Stappenbeck (1905) reassigned it to a new genus as *Stephanospondylus pugnax*. Although the dentition and/or vertebrae of both forms clearly justifies a diadectid assignment, the lack of additional discoveries has not permitted detailed comparisons with the better known diadectids, particularly *Diadectes* of North America, and both of the German taxa remain poorly defined (Romer, 1925).

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During a period of nearly two decades, four specimens assignable to *Diadectes* as a new species have been recovered from a sandstone quarry known as the Bromacker locality that lies in the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, in the middle part of the Thuringian Forest near Gotha, central Germany (Berman and Martens, 1993; Sumida et al., 1996). The first specimen discovered, consisting of a nearly entire, slightly disarticulated post-cranial skeleton, was collected by Martens and Schneider in 1979 during an exploratory excavation at the Bromacker quarry, but was misidentified as possibly a limnoscelid diadectomorph (Martens, 1980, 1988, 1989; Martens et al., 1981). In the summer of 1991, Martens discovered a nearly complete, isolated small skull of a juvenile specimen which he identified as a diadectid in a brief note (Martens, 1992). Two closely associated adult specimens were collected by the authors in the summer of 1993. One consists of a nearly complete, articulated skeleton with an excellently preserved skull (designated here as the holotype of a new species) and the other the greater portion of an articulated postcranium. Collectively, these specimens represent the first occurrence of *Diadectes* outside of the Lower Permian of North America.

The Bromacker *Diadectes* is part of a diverse assemblage of terrestrial or semiterrestrial amphibians and reptiles represented by articulated skeletons from the Bromacker locality (Martens, 1980, 1988, 1989; Boy and Martens, 1991; Berman and Martens, 1993; Sumida et al., 1994, 1996). To date, three Bromacker vertebrates have been described: 1) a single, nearly complete skeleton of a new genus of protorothyridid amniote, *Thuringothyris mahlendorffae* Boy and Martens, 1991; 2) two specimens of the seymouriamorph amphibian *Seymouria* were tentatively referred to *S. sanjuanensis* Vaughn, 1966 (Berman and Martens, 1993); and 3) a skull and partial, articulated postcranium representing a new genus and species of the amphibian family Trematopidae (Sumida et al., 1994). *Seymouria* and trematopids are known otherwise only from the Early Permian and Permo–Pennsylvanian, respectively, of North America.

For over a century the Bromacker locality has been well known as a very important source of excellently preserved tetrapod trackways preserved in the Tambach Sandstone of the Tambach Formation (Pabst, 1896, 1908; Müller, 1954, 1969; Haubold 1971, 1973). Vertebrate skeletal remains, however, eluded detection at Bromacker until 1974 (Martens, 1980). All of the vertebrate skeletal specimens so far collected from Bromacker have come from fluvial red-bed facies immediately above the sandstones yielding the trackways and are quite similar to those deposits which have yielded the vast majority of the Lower Permian and Permo–Pennsylvanian vertebrates of the United States (Martens, 1975, 1982, 1988, 1989; Martens et al., 1981; Berman and Martens, 1993; Sumida et al., 1996). With the exception of Bromacker, terrestrial or semiterrestrial vertebrates from Permian red-bed deposits of the Rotliegend or their equivalent in central and western Europe are quite rare and include most notably the primitive synapsids, *Haptodus* (Paton, 1974; Currie, 1979; Laurin, 1994), *Ophiacodon* (Paton, 1974), and *Sphenacodon* (Paton, 1974) from England and *Casea* (Sigogneau-Russell and Russell, 1974) from France.

The apparent uniqueness of Bromacker among European localities has been explained as possibly an artifact of collecting (Martens, 1989; Berman and Martens, 1993; Sumida et al., 1996). The red-bed exposures of the Upper Rotliegend are very poor and have been commonly perceived as representing an inhospitable dry climate that was not conducive to preservation of skeletal remains. As a result,

relatively little energy has been devoted to their exploration, and, as a consequence, they have yielded few vertebrates. Alternatively, intensive prospecting has focused on the highly fossiliferous lacustrine grey sediments and black shales of the Lower Rotliegend that reflect limnetic environments. These deposits, in which are found the well-known tetrapod localities as Niederhaeslich, Friedrichroda, and various Saar-Nahe sites such as Lebach, have yielded a great number and variety of obligatory aquatic amphibians, but only very rarely terrestrial or semiterrestrial tetrapods (Milner and Panchen, 1973; Milner, 1993).

Two important conclusions have been suggested (Berman and Martens 1993; Sumida et al., 1996; Berman et al., 1997) to explain the high degree of commonality between the Bromacker tetrapod assemblage and those of the Lower Permian red-bed deposits throughout the United States: 1) similar environments, as represented by typical fluvial red-bed facies, are being sampled; and 2) an absence of major physical and biological barriers during the Early Permian allowed faunal interchange across northern Pangaea.

The striking similarities between the Bromacker assemblage and those of North America have also brought into question the widely accepted assessments of the biostratigraphic position and age of the Tambach Formation, lowermost formational unit of the Lower Permian Upper Rotliegend of the Tambach Basin in the midregion of the Thuringian Forest of central Germany. The Rotliegend, as well as its lower and upper subdivisions (in western Europe the lithostratigraphic terms Autunian and Saxonian are commonly used in place of Lower and Upper Rotliegend, respectively), is a traditional lithostratigraphic unit that refers to continental beds considered to be entirely or in great part Lower Permian and to overlie Upper Carboniferous Stephanian deposits in central Europe. In the region of the Thuringian Forest the Upper Permian marine Zechstein overlies in places the Rotliegend. Certain elements of the Bromacker assemblage, particularly *Seymouria* cf. *S. sanjuanensis*, *Diadectes*, and trematopid, strongly suggest an earliest Permian Wolfcampian age for the Tambach Formation. This, in turn, indicates that most or possibly all of the underlying Lower Rotliegend in the Thuringian Forest region should be reinterpreted as Upper Carboniferous (Berman and Martens, 1993; Sumida et al., 1996), rather than the widely accepted Lower Permian.

The following acronyms are used to refer to institutional repositories of specimens: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNG, Museum der Natur, Gotha, Germany; UCMP, Museum of Paleontology, University of California, Berkeley, California.

Anatomical structures are identified by the following abbreviations: a, angular; af, anterior fenestra; ar, articular; ati, atlantal intercentrum; atn, atlantal neural arch; axc, axial centrum; axi + atp, axial intercentrum plus atlantal pleurocentrum; axn, axial neural arch; bo, basioccipital; c, coronoid; c3, centrum 3; d, dentary; ec, ectopterygoid; en, external naris; fp, footplate of stapes; i3, intercentrum 3; in, internal naris; j, jugal; l, lacrimal; m, maxilla; mf, medial fenestra; n, nasal; na4, neural arch 4; oc, occipital condyle; osp, ossified plate of stapes; ot, otic trough; p, parietal; pal, palatine; pat, proatlas; pm, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; pra, prearticular; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qf, quadratojugal foramen; qj, quadratojugal; r1, atlantal rib; r2, axial rib; r3, r4, presacral ribs 3 and 4; sa, surangular; sf, stapedial foramen; sm, septomaxilla; sop, supraoccipital–opisthotic; sp, splenial;

sq, squamosal; ss, stapedial shaft; st, supratemporal; t, tabular; v, vomer; I–V, carpal digits.

SYSTEMATIC PALEONTOLOGY

Order Diadectomorpha
Family Diadectidae
Genus *Diadectes* Cope 1878
Diadectes absitus, **new species**

Holotype.—MNG 8853, greater part of an articulated skeleton with skull contained in two adjoining blocks and lacking the following: large portions of the tail; interclavicle; left shoulder girdle, forelimb, and manus; right radius, ulna, and manus; left hindlimb and pes; and most of the right pes. A disarticulated right clavicle preserved directly above the cervical vertebrae was removed. A string of four distal caudal vertebrae lying a short distance to the right of the midlength region of the presacral column almost certainly belongs to the holotype.

Paratypes.—MNG 8747, greater part of skull with lower jaws; MNG 7721 and 8978, greater portions of articulated and partially articulated, respectively, postcranial skeletons.

Horizon and Locality.—Uppermost level of 60 m-thick Tambach Sandstone of the Lower Permian Tambach Formation, Upper Rotliegend, in the Bromacker locality of the middle part of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany.

Diagnosis.—Can be distinguished from all other *Diadectes* species by the following autapomorphic features: 1) postfrontal chevron-shaped, with its posterior apex penetrating deeply into anterior margin of parietal; 2) postorbital has very narrow entrance into orbit; 3) abrupt, dorsalward, step-like retreat of anterior portion of jugal from the free, ventral margin of the skull; 4) lower jaw subcircular in cross-sectional shape at level of coronoid eminence with the height and width being nearly equal; and 5) dentary lacks a prominent labial parapet lateral to the cheek teeth and in its place is a wide, dorsally facing platform. The following plesiomorphic features distinguish *Diadectes absitus* from all other members of the genus: 1) dorsal process of premaxilla long and narrow, extending to a level beyond the posterior margin of the external naris; 2) prefrontal extends well beyond the level of the anterior margin of the frontal; 3) postorbital forms for most of its posterior extent a tapering, triangular process that ends in a very narrow contact with the supratemporal; and 4) basicranial joint remains open and mobile in adults.

Etymology.—Latin, *absitus*, meaning distant, apart, or remote, referring to its distant occurrence from all other known members of the genus that occur in North American.

Description.—**Skull Roof.** The skull of *Diadectes absitus* conforms very closely to descriptions of North American members of this unique genus. For this reason the description that follows, including the postcranium, is mainly restricted to those features that are either at variance with previous accounts (Olson, 1947, 1950; Watson, 1954; Lewis and Vaughn, 1965; Berman et al., 1992) or are not obvious from the illustrations presented here or elsewhere of North American species. With this approach in mind, in all the figures presented here to illustrate the cranial anatomy of *D. absitus* the identification of structures has been limited mainly to those in which possible confusion may occur. In addition, cranial sutures have been drawn on the skulls with ink.

The skulls of the holotype MNG 8853 and the paratype MNG 8747 (Fig. 1–8) are approximately the same length (13.0 cm), but in other measurements, particularly transverse dimensions, the holotype is 9–12% larger. The holotypic skull is complete and has undergone minor dorsoventral crushing of the right side and occiput and lateral crushing of the left side. The paratypic skull MNG 8747, on the

other hand, has been crushed moderately dorsoventrally, and considerable amounts of bone have been lost from the cheek regions. As in the North American species, the roofing bones of both skulls are thick and porous, with a high degree of relief, particularly on the table portion, where well-developed, irregular prominences are created by a network of prominent, smooth channels or grooves. Also as in the North American species, these features are more prominent in the smaller, less mature MNG 8747 than in the holotypic skull.

The premaxillae are preserved in both skulls, but only in MNG 8853 (Fig. 3, 4) are the dorsal processes well preserved. They are narrow, tapering slightly to blunt points as they extend a considerable distance onto the dorsal surface of the skull to a level well beyond the posterior margin of the external nares. Each premaxilla possesses four procumbent, incisiform teeth which are subequal in size except for the fourth being considerably smaller. Although the premaxillary teeth of MNG 8853 are all present, only their labial surfaces are visible. In MNG 8747 only the bases of the teeth remain except in the right premaxilla, where the fully erupted third is missing the tip of the crown and only the crown of the partially erupted fourth is visible. The crowns of replacement teeth are also visible in the lingual pits of the second tooth of the right premaxilla and the first and third of the left. The teeth are distinctly procumbent and incisiform. The bases are oval in cross section with the long axis directed posteromedially, whereas the lingual surface of the distal portions are broadly concave, giving them a chisel-like appearance.

The paired nasals and frontals are narrowly rectangular and nearly equal in their dimensions. The frontals, however, are slightly shorter and gradually widen slightly posteriorly. In both skulls the great width of the parietals is due to a pronounced, well-defined rectangular lateral lappet that replaces, or represents the incorporation of, the intertemporal bone (Berman et al., 1992). In MNG 8747 a narrow, spike-like projection of the posterior margin of the parietal partially separates the tabular and supratemporal. In MNG 8853 the projection is much broader and subrectangular, but this may be due in part to crushing in the occipital region. The postparietal is a single, anteroposteriorly narrow, rectangular bone, which in MNG 8853 has a width approximately four times its midline length. Approximately one-third of the postparietal surface area, extending along its anterior margin, is exposed on the skull table, whereas the remaining posterior portion of the bone is angled abruptly downward onto the occiput to overlap the dorsal margin of the supraoccipital. In MNG 8747 the posterior portion of the postparietal slopes ventrally from the skull table at about 45°, whereas in MNG 8853 the surface is vertical. Although the prefrontal extends noticeably beyond the level of the anterior margin of the frontal in both skulls, the extension is greater in MNG 8853. The chevron-shaped postfrontal forms the posterodorsal margin of the orbit, with the posterior apex penetrating deeply into the anterior margin of the parietal.

Description of the cheek bones is based almost exclusively on MNG 8853. The postorbital has a narrow entrance into the posterior corner of the orbit. The greater portion of the postorbital forms a posteriorly narrowing, triangular process that extends along the lateral margin of the parietal lappet to within a short distance of the expanded otic, or temporal, notch. The postorbital ends in a narrow contact with the supratemporal, thus preventing contact between the lateral lappet of the parietal and squamosal. At its anterior contact with the premaxilla the maxilla has a short, narrow, dorsally directed, process-like extension that enters the external naris. Posteriorly the maxilla extends to about the level of the midlength of the orbit.

Only the dentition of the right maxilla of the juvenile skull MNG 8747 is fully exposed and well preserved, and includes 11 teeth at various stages of replacement: teeth 2, 4, 6, 7, and 9 are fully erupted, ankylosed, and show wear on the lingual cusp and on some of the central cusps as well; teeth 1, 5, and 10 are fully erupted, ankylosed, and show no wear; and teeth 3, 8, and 11 are partially erupted and not ankylosed. The crowns of replacement teeth are visible in the lingual pits of the second, fourth, and ninth teeth. The maxillary dentition is essentially identical to that of other members of the genus. Yet, a description providing some details is warranted, because *Diadectes* exhibits marked developmental growth stages of the marginal dentition that differ from those in the very closely related, Late Pennsylvanian *Desmatodon* (Vaughn, 1969, 1972; Berman and Sumida, 1995). Although all the maxillary teeth in MNG 8747 are expanded transversely, they are positioned so that the labial edge of each tooth lies well anterior to the lingual edge. The first two teeth are slightly longer and more incisiform than the succeeding maxillary teeth, giving them a morphology intermediate between those of the premaxilla and the more posterior, molar-like cheek teeth. The labial cusp is essentially absent, the posteromedial surface of the well-developed central cusp is broadly concave, and the lingual cusp is weakly developed. The crown of the third tooth is only partially erupted, but also appears to be incisiform. The remaining teeth of the series increase in size to the sixth tooth and then decrease to the end of the series. The cheek teeth exhibit the typical molar-like structure seen in other species of *Diadectes*, although their degree of development or "molarization" clearly reflects a juvenile stage of growth (Berman and Sumida, 1995). The subconical central cusps of the cheek teeth are very pro-
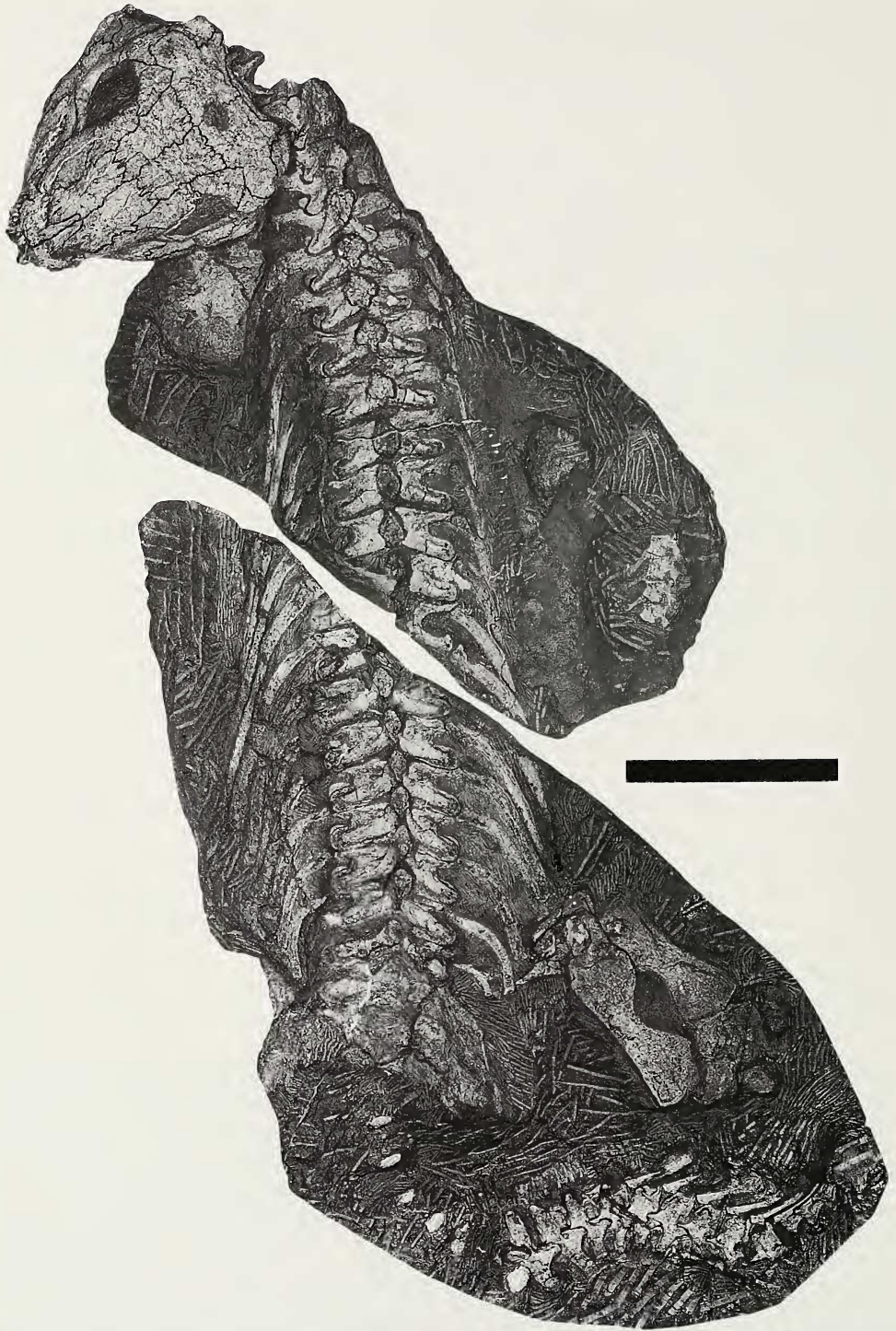
Fig. 1.—*Diadectes absitus*, holotype (MNG 8853). Greater part of articulated skeleton exposed mainly in dorsal view as preserved in two blocks and showing the skull, vertebral column except for large

nounced and represent possibly half the height of the crown, whereas the lingual and labial cusps are poorly developed and would be more accurately described as "shoulders." The lingual cusps are much more sharply defined than the labial cusps, as the bases of the central cusps are much more expanded laterally than they are medially. The sixth and largest of the molariform cheek teeth measures 7.0 mm in transverse width, 3.7 mm in anteroposterior length, and 5.0 mm in height. The spacing between cheek teeth 4 through 7 is about 1.0 mm. Enough of the right maxillary dentition of MNG 8853 is exposed laterally to indicate the presence of at least ten teeth plus spaces for two more. The teeth appear to exhibit the same serial changes as in MNG 8747.

The lacrimal and jugal are preserved only in MNG 8853. Their contribution to the suborbital bar on the right side of the skull is unusual, however, in that the suborbital process of the jugal appears to form the entire ventral border of the orbit. The typical condition for this structure is seen on the left side of the skull, where the suborbital process of the jugal is shorter, and the ventral orbital rim is completed anteriorly by a short posterior, suborbital process of the lacrimal. The jugal's contribution to the ventral margin of the skull exhibits an abrupt, step-like dorsalward retreat just anterior to the quadratojugal. This feature is especially pronounced in the left jugal.

Only the right septomaxilla of MNG 8853 is sufficiently well preserved and accessible for description (Fig. 4), and in general conforms to that described in Early Permian synapsids (Romer and Price, 1940; Wible et al., 1990). It is subrectangular in outline and lies deep within the external naris. However, because its margins are extremely thin and a major crack through the skull extends along its ventral contact with the premaxilla, the exact outlines of this element are difficult to discern. The posterior margin appears to contact the lacrimal, the dorsal margin nearly reaches the nasal, but their proximity may have been exaggerated by dorsoventral crushing of the skull, and the anterior margin ends free at about midlength of the external naris. Basically the septomaxilla is deeply bowed medially, so that its dorsal and ventral margins curve outward to the facial surface of the skull. Most prominent is a narrow, pillar-like structure, described as the dorsal process in primitive synapsids, which extends posterodorsally, joining the lateral lips of the dorsal and ventral margins of the septomaxilla. The outer surface of the dorsal process may have had a facial exposure. The dorsal process is pierced by an anteroposterior canal, the septomaxillary canal, which in primitive synapsids is believed to have transmitted branches of the superior labial nerve and artery (Wible et al., 1990). Crushing of the skull appears to have resulted in a small amount of lateral overlap of the posterior margin of the septomaxilla by the lacrimal. This may have obscured the presence of a septomaxillary foramen which is normally present at the union of the two elements.

MNG 8853 and 8747 exhibit features of the squamosal and quadratojugal (Fig. 5, 6, 7B, 9A) either overlooked or not preserved in North American specimens described by previous authors. Not mentioned in previous descriptions is a broad flange of the squamosal that projects medially and slightly posteriorly from nearly the entire length of the posterior or otic margin of its facial exposure that can be referred to as the medial flange. In MNG 8747 most of the facial exposure of the right squamosal has been lost, revealing the medial flange. It has an extensive, overlapping suture with all but a narrow ventral margin of the anterior surface of the portion of the quadrate which forms the transversely wide, anterior wall of the otic notch. In Figure 9A, however, only the lateral edge of the medial flange of the squamosal is visible. As seen in the skull MNG 8853 (Fig. 5, 6, 7B), the posterior surface of the medial flange of the squamosal is not overlapped entirely by the quadrate, and a narrow strip along its lateral margin is exposed in occipital view. Further, the facial surface of the otic margin of the squamosal is extended posteriorly 2 or 3 mm into a knife-like edge whose inner surface curves abruptly medially to become the medial flange. The quadratojugals are represented by only those in the holotypic skull MNG 8853, but only the right one is well preserved and accessible. It completes the sculptured, posteroventral rim of the otic notch, ending in a small, free, triangular, medially directed process. Below and just anterior to the sculptured medial process is a narrow, nonsculptured, sharply wedge-shaped medial extension of the quadratojugal that enters the anterior wall of the otic notch to form the medial margin of the quadratojugal foramen before ending just above the lateral condyle of the quadrate. In MNG 8747 the facial exposure of the right quadratojugal has been lost and only a broad medial flange like that of the squamosal remains. The medial flange overlaps not only the ventral margin of the anterior surface of the portion of the quadrate forming the anterior wall of the otic notch, but also the greater portion of the anterior surface of the medial flange of the squamosal.

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portions of caudal series, iliac blades, and right tibia, fibula, and proximal portion of pes. A series of four distal caudals presumed to belong to the holotype lies to the right of the midpresacral region of column. Scale = 10 cm.

Fig. 2.—Reverse side of two blocks seen in Figure 1 containing *Diadectes absitus*, holotype (MNG 8853) and showing the skull, anterior cervical vertebrae, right femur, and puboischiatic plate in ventral view, right cleithrum and scapulocoracoid in lateral view, and right humerus with distal expansion in ventral view. Scale = 10 cm.
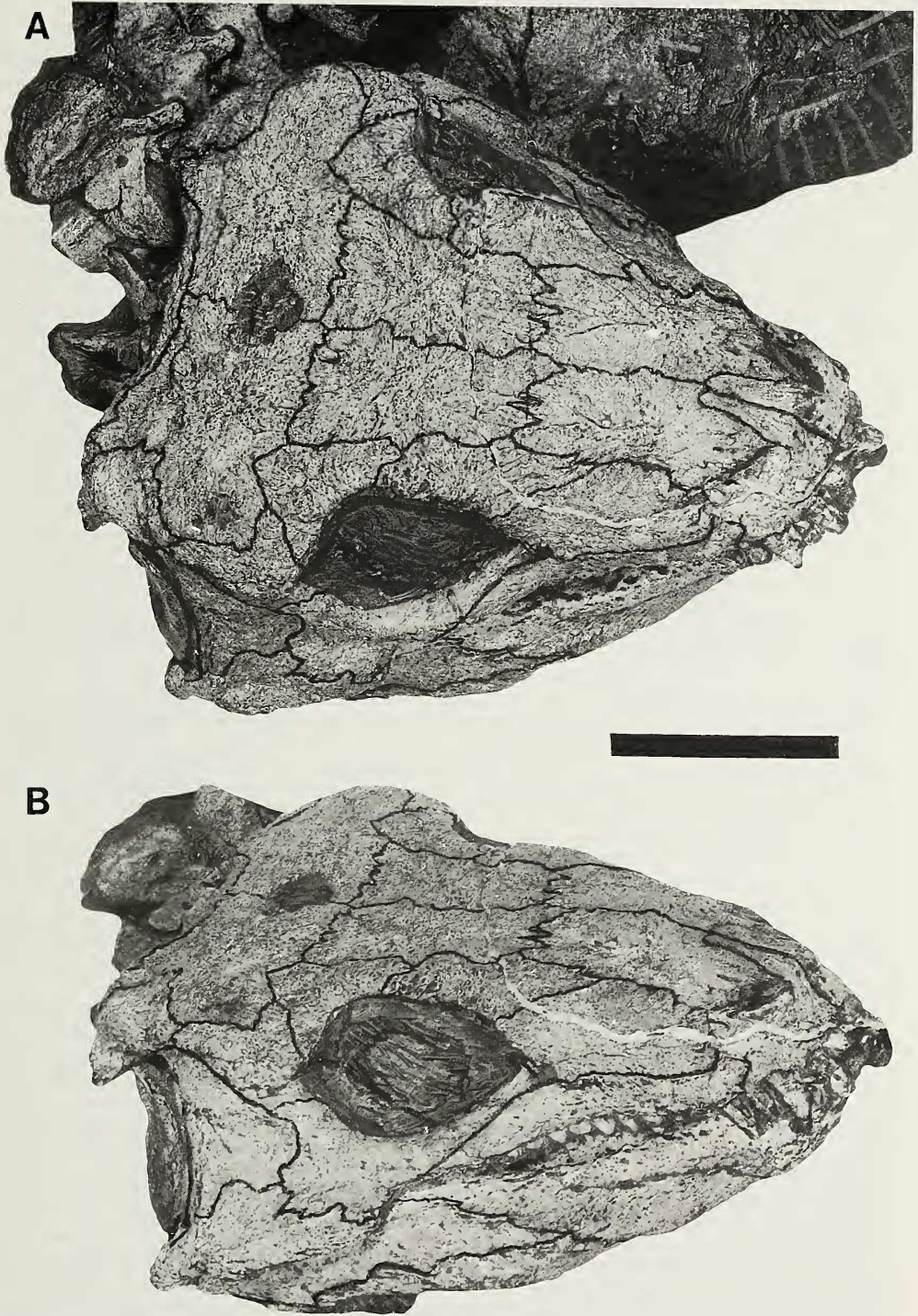
Fig. 3.—*Diadectes absitus*, holotype (MNG 8853). Skull in A, dorsal and B, lateral views. Scale = 4 cm.
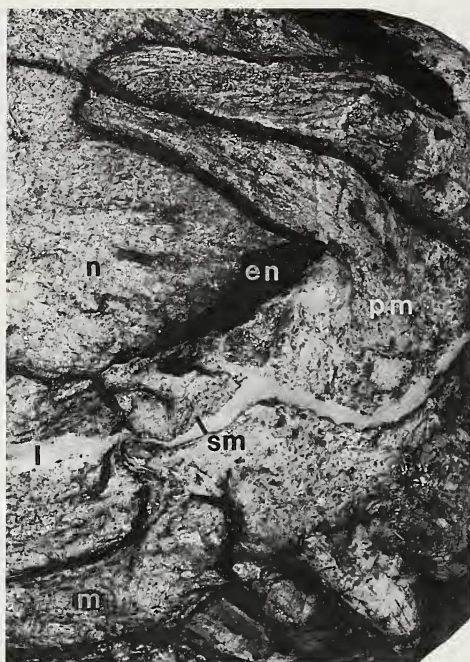
Fig. 4.—*Diadectes absitus*, holotype (MNG 8853). Right nasal region of skull in lateral view. Scale = 2 cm.

Extending posteriorly from the end of the spike-like projection of the posterior margin of the parietal is a distinct suture that continues to the distal end of the sculptured, downturned, posterolateral, horn-like extension of the skull table. This suture marks the contact between the tabular and the supratemporal. Whereas the tabular and supratemporal occupy subequal portions of the sculptured, horn-like extension of the skull table in MNG 8747, the supratemporal forms most of this structure in the larger MNG 8853. Both *D. absitus* skulls reveal that the ventral surface of the distal end of the horn-like extension of the supratemporal, that forms the posterodorsal margin of the otic notch, has a substantial contact with the dorsal edge of the distal end of the paroccipital process. From its sculptured contribution to the skull-table horn, the tabular extends medially and slightly anteriorly onto the occipital surface of the skull as a smooth plate of bone. This portion of the tabular contacts most of the dorsolateral margin of the supraoccipital–opisthotic complex of the braincase (Fig. 7B). From near the distal end of the paroccipital process, this contact arches slightly medially to reach the lateral margin of the occipital portion of the postparietal.

Palate. The palate is possibly the most poorly known region of the skull of *Diadectes*. Olson (1947) presented the most recent and detailed reconstruction of the palate, based on several individuals, yet many features remain undescribed. The palate of *D. absitus* is best preserved and exposed on the right side of skull MNG 8747 (Fig. 10), although some breakage and loss of bone has slightly obscured the sutural contacts of the palatine and ectopterygoid. In MNG 8853 the right pterygoid, ectopterygoid, and posterior half of the palatine are exposed and well preserved, as well as part of the left pterygoid (Fig. 7A). Anteriorly the vomer forms a ventrally thickened, midline, ridge-like premaxillary process that ventrally overlaps the vomerine process of the premaxilla. The premaxillary processes are very narrowly separated and their distal ends are slightly forked. Although much of the posterior contact of the vomers with the pterygoids in MNG 8747 is poorly defined, it is still traceable. Posterior to the premaxillary process the vomer continues along the midline as a dorsoventrally thickened ridge to the level of the sixth maxillary tooth and supports a single row of eight teeth. This interpretation agrees with Olson's (1947) reconstruction. From the dorsolateral margin of the premaxillary process a flat, wing-like, posterolateral extension of the vomer forms much of the anterior medial border of the long, narrow internal naris. The posterolateral wing of the vomer is not shown in Olson's (1947) reconstruction.

Anteriorly the palatal ramus of the pterygoid extends lateral to the adjacent, midline, tooth-bearing

ridge of the vomer, contacting the posteromedial margin of the posterolateral wing of the vomer. Although most of the lateral margin of the pterygoid is hidden from view by the palatine, it is clearly highly unusual in contributing to the medial margin of the internal naris, forming as much as the posterior half of the medial border of the opening, and in preventing a vomer–palatine contact. The palatal rami of the pterygoids unite along the midline for much of their length, allowing for only a short, narrow interpterygoid vacuity posteriorly. The medial tooth-bearing ridge of the vomer is continued posteriorly by the pterygoid, which contributes ten more well-developed teeth to the series. The double row of midpalatal teeth of the paired vomers and pterygoids have cylindrical bases and sharply pointed conical crowns. The teeth of both rows increase in size posteriorly from a vertical height of about 0.03 to 1.05 mm except for a marked decrease in the last three teeth. The midline vomer–pterygoid tooth rows and marginal dentitions lie at the same horizontal plane and below the slightly vaulted palatal surfaces.

The transverse flange of the pterygoid is subrectangular in ventral outline, expanding somewhat distally along its free, posterior margin. In MNG 8747 the ventral surface of the process thickens so greatly distally, that in lateral view its distal end projects well below the plane of the palate as a broadly triangular, vertical shelf (Fig. 9A). The anterior margin of the flange is defined sharply, particularly in MNG 8853, by a shallow, dorsalward, step-like elevation to the ventral surface of the palate proper. The distal half of the anterior margin of the flange contacts the ectopterygoid. In both *D. absitus* skulls the transverse flange of the pterygoid lacks teeth and, whereas the ventral surface of the process in MNG 8853 is slightly textured, that in MNG 8747 is smoothly finished. A shagreen of minute denticles is visible along the medial margin of the right palatal ramus in MNG 8747 from the base of the transverse flange to the posterior end of the medial row of teeth. The interpterygoid vacuity is closed posteriorly on either side of the midline by a very broad, posteromedially directed, flange-like process of the pterygoid, referred to here as the basal process. All but a small, triangular, anteromedial area of the ventral surface of the basal process is occupied by a slightly depressed articular facet that faces mainly ventrally and slightly posteriorly to receive the basipterygoid process of the braincase. The quadrate ramus of the pterygoid extends posteriorly to the level of the quadrate condyle. Beginning immediately behind the transverse flange the ventral edge of the ramus forms a narrow, shelf-like lateral flange that gradually tapers posteriorly to its termination at about three-fourths the length of the ramus. A short distance posterior to the basal articulation a small, narrow, convex flange projects nearly dorsally from near the ventral margin of the central portion of the internal surface of the quadrate ramus. This flange is similar to that described in *Limnoscelis* as the arcuate flange (Romer, 1946; Fracasso, 1983).

The unique structure of the palatine in North American *Diadectes* (Olson, 1947; Berman and Sumida, 1995) is duplicated in the *D. absitus* (Fig. 7A, 10). There is a pronounced, arcuate, secondary palatal shelf that extends medially from its contact with the inner margin of the maxillary alveolar shelf and ventral to the primary palatal shelf of the true palate. In palatal view the secondary shelf partially obscures most of the contact between the primary palatal shelf of the palatine and pterygoid. A ventrally thickened, rectangular process, referred to here as the posteromedial process, extends from the posterior end of the primary palatal shelf of the palatine. Proximally the posteromedial process of the palatine nearly closes the channel formed between the primary and secondary palatal shelves of the palatine. In MNG 8747 the posteromedial process of the palatine appears to reach nearly the transverse flange of the pterygoid, whereas in MNG 8853 it is continued to the transverse flange by a short, complementary process of the pterygoid. The secondary palatal shelf of the palatine is continued a short distance posterolaterally by the ectopterygoid to the free, lateral margin of the palate. From here the shelf is continued by a short, narrow, posterior extension of the ectopterygoid that curves slightly ventrally to contact the distal end of the anterior margin of the transverse flange of the pterygoid. A small portion of the ectopterygoid posterior and medial to its contribution to the secondary palate is depressed abruptly dorsally to form a shallow concavity that is bordered medially by the posteromedial process of the palatine and posteriorly by the transverse flange of the pterygoid. In Olson's (1947:fig. 3) reconstruction of the palate of *Diadectes* he illustrated the depression at the junction of the ectopterygoid, pterygoid, and palatine as a circular pit, but noted that in some specimens this depression appears to penetrate the bone as a fenestra. Interestingly, he commented (p. 16) that the depression or pit lies in the position of the infraorbital fossa and may represent an incipient development of this opening.

Palatoquadrate. Only the quadrate (Fig. 5–7, 9, 10) of this complex has been exposed and consists basically of three major components: the condyle and two vertical sheets or laminae that arise from the condyle. One lamina, which can be referred to simply as the otic or temporal lamina, extends for a considerable height above the condyle as the transversely wide, subrectangular plate that forms the anterior wall of the otic notch. Its summit contacts the ventral surface of the supratemporal and, as shown by Watson (1954), possesses a short process at its dorsomedial margin which ends in a gently
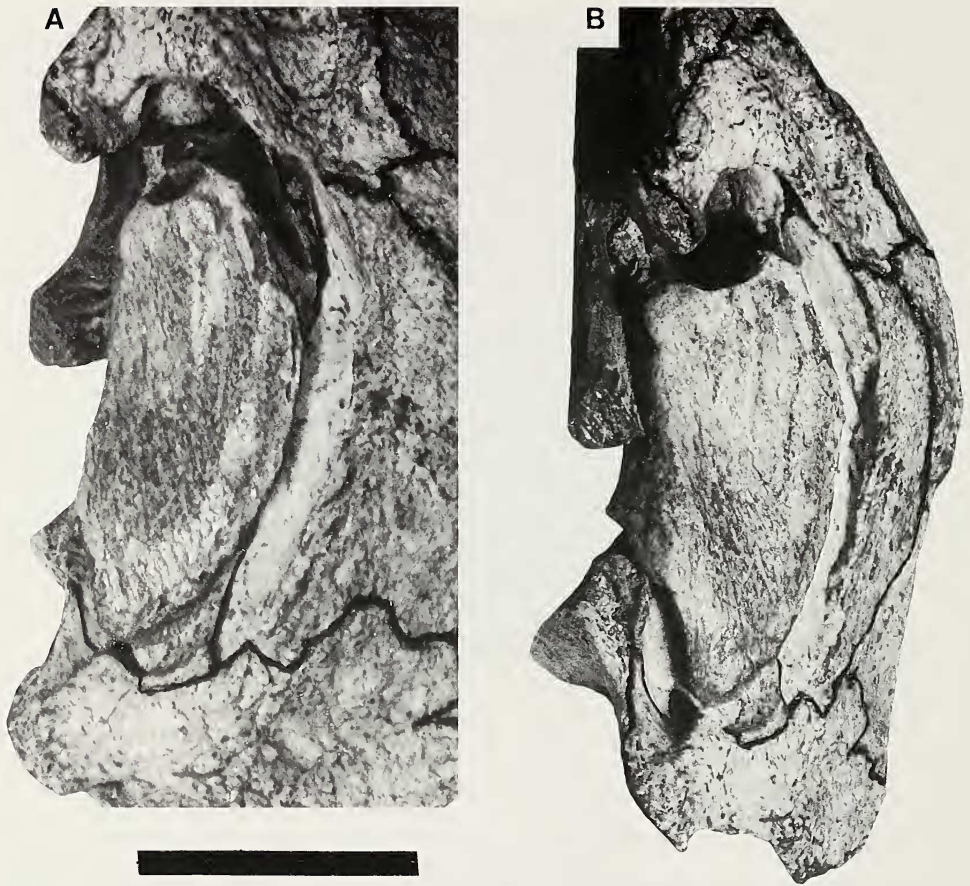
Fig. 5.—*Diadectes absitus*, holotype (MNG 8853). Right otic region in A, posterolateral and B, occipital views. Scale = 2 cm.

convex oval face that inserts into a conforming facet on the lateral surface of the prootic. At the ventromedial corner of the posterior surface of the otic lamina, just above the medial lobe of the condyle, is a short, well-defined subcircular protuberance, the quadrate boss. Lateral to the boss the quadrate forms all but the lateral margin of the quadratojugal foramen.

The second, vertical lamina of the quadrate, the dorsal process or lamina, extends anteriorly and slightly medially from the medial margin of the otic lamina, so that an approximate right angle is formed anterolaterally between them. Proximally the dorsal lamina may have reached the height of the otic lamina, but tapers somewhat anteriorly as the ventral margin of its medial surface overlaps the lateral surface of the quadrate ramus of the pterygoid. This contact is very extensive anteroposteriorly, as the dorsal lamina of the quadrate extends to approximately the level of the posterior margin of the transverse flange of the pterygoid (Fig. 9A). The greater distal portion of the ventral edge of the dorsal lamina inserts in a very shallow groove on the dorsal surface of the narrow, lateral flange of the quadrate ramus of the pterygoid.

Braincase. In MNG 8853 the only portion of the braincase visible in palatal view is the right side of the basiparasphenoid complex, whereas dorsoventral crushing has resulted in considerable telescoping and distortion of the braincase bones exposed on the occiput. On the other hand, these regions of the braincase in MNG 8747 are relatively well preserved and exposed (Fig. 9B, 10), and provide almost entirely the basis for the description that follows. The parasphenoidal rostrum is visible as a keel-like structure that extends a short distance across the interpterygoid vacuity. On the midline of its proximal end is a small, ventrally projecting protuberance. The well-developed basipterygoid processes are subrectangular in outline, constricting somewhat at their base. They project anterolaterally
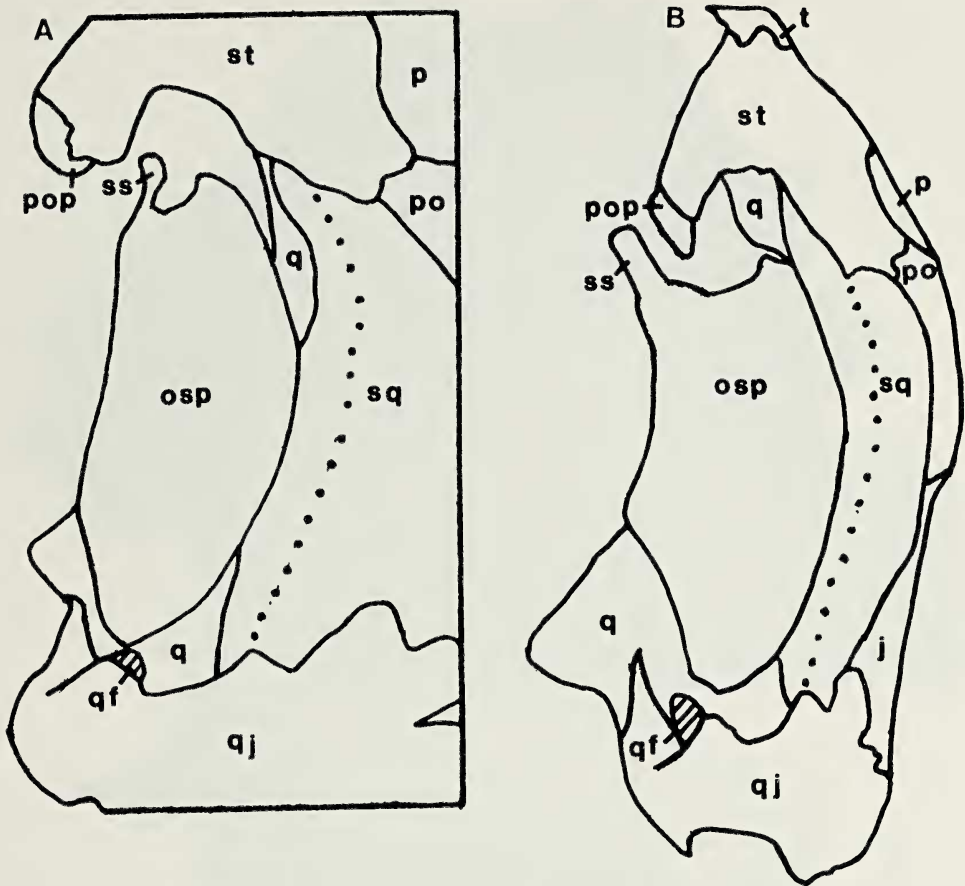
Fig. 6.—Outline sketches of views A and B of Figure 5 to indicate individual elements and other structures. Dotted line marks union of facial and occipital surfaces of squamosal.

and slightly ventrally, with their articular facets facing dorsally and slightly anterolaterally. A mobile, basicranial joint was undoubtedly present in both MNG 8747 and 8853. Posterior to the basipterygoid processes the smooth, ventral surface of the basiparasphenoid continues a short distance before expanding on either side of the midline as thin, free-edged, ventrally arching sheets that extend posterolaterally to form long, triangular projections, the cristae ventrolaterales. A very narrow space separates the posterior edges of the cristae from the overlying basiparasphenoid complex proper which continues a short distance posteriorly to a transverse, feathered contact with the basioccipital. In both *D. absitus* skulls the occipital condyle faces strongly posteroventrally, which may be due in small part to dorsoventral crushing. In posterior view the condyle is semicircular in outline, with rounded dorsolateral corners and a slight, middorsal concavity. In MNG 8853 the articular surface is essentially flat, whereas in MNG 8747 there is a deep, central notochordal pit.

The prootics are exposed in palatal view of the skull MNG 8747 (Fig. 10). They arise anteriorly from near the base of the basipterygoid process, with which they are indistinguishably fused, and extend posterolaterally for a considerable distance immediately adjacent to the lateral margins of the cristae ventrolaterales as wing-like sheets. Distally their incompletely preserved medial margins become very thin and appear to have ended in an abutment contact with the lateral edges of the cristae ventrolaterales. The thickened lateral margins of the prootics curve dorsally, and, although their extent in this direction can be exposed only a short distance, it is assumed that they continued as the lateral walls of the braincase. Just posterior to the palatal exposure of the right prootic in MNG 8747 (Fig. 10) is a large, stout, crescent-shaped structure that projects ventrally from near the base of the par-
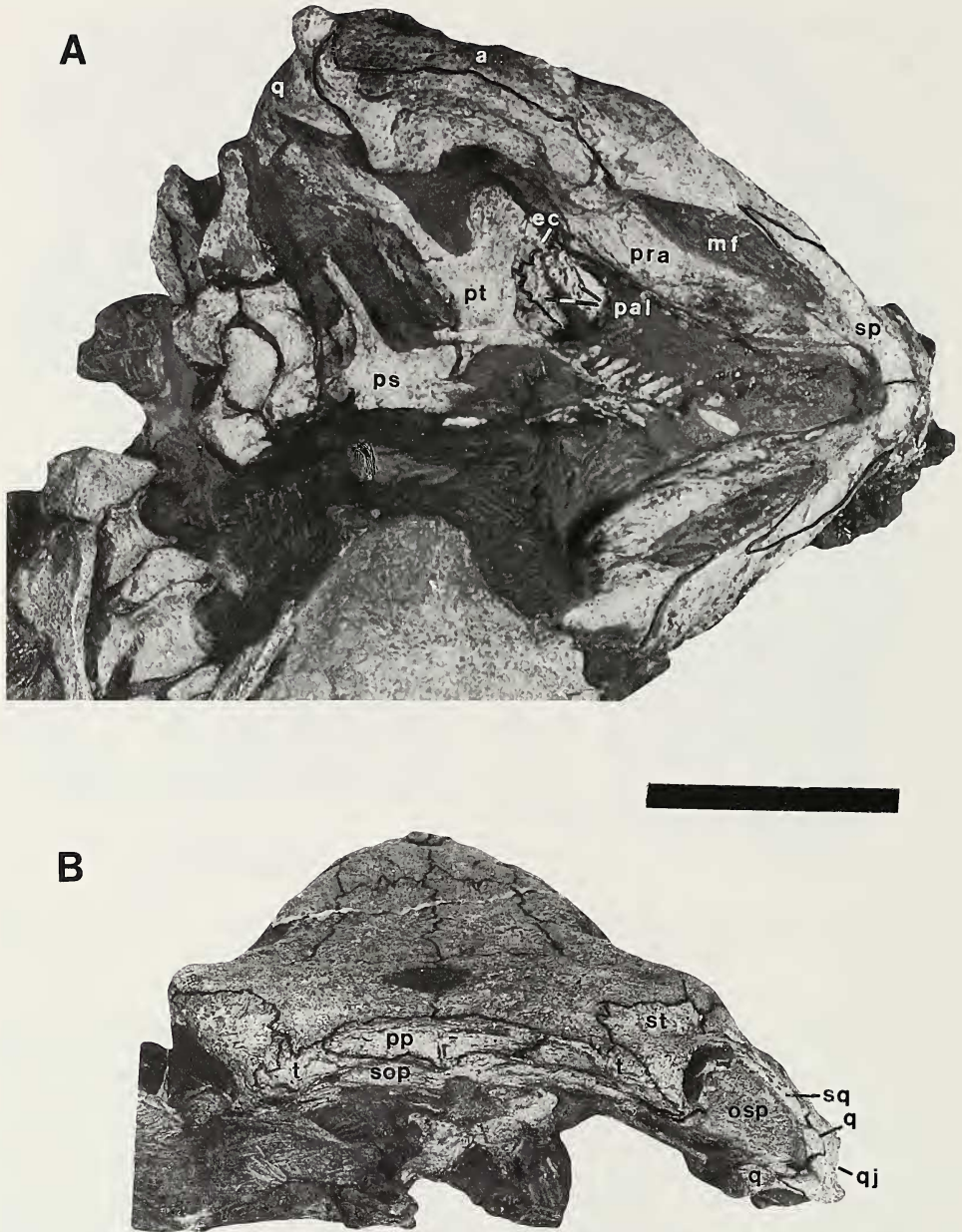
Fig. 7.—*Diadectes absitus*, holotype (MNG 8853). Skull in A, ventral and B, occipital views. Scale = 4 cm.

occipital process of the opisthotic. Its coarsely textured, concave surface faces posteromedially and ventrally. This structure, which has been termed the otic trough (Fracasso, 1983; Berman et al., 1992), has been identified in *Limnoscelis* and North American *Diadectes*, as well as in primitive synapsids, and described as being formed entirely by the opisthotic and projecting ventrolaterally from the posterior border of the fenestra ovalis (Fracasso, 1987; Berman and Sumida, 1990; Berman et al., 1992). Although a function has not been ascribed to the otic trough, the in-place exposure of the right stapes
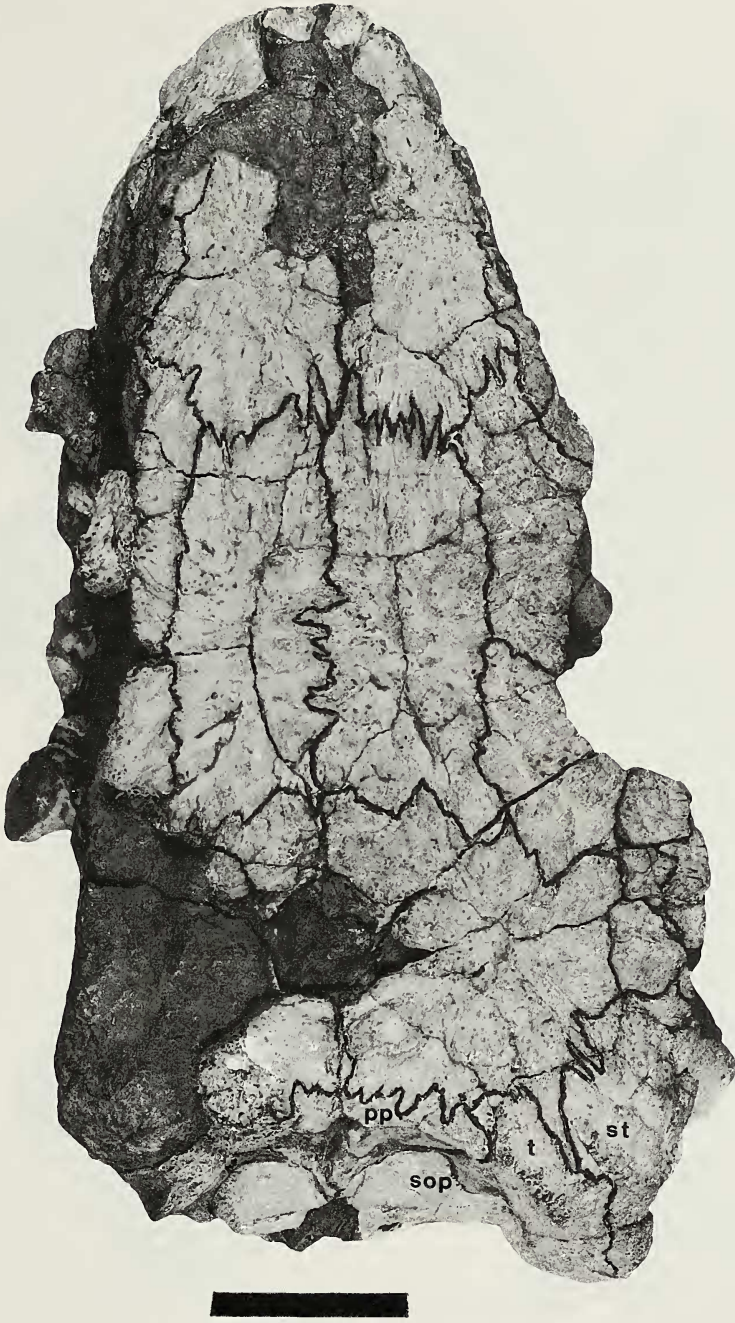
Fig. 8.—*Diadectes absitus*, paratype (MNG 8747). Skull in dorsal view. Scale = 2 cm.
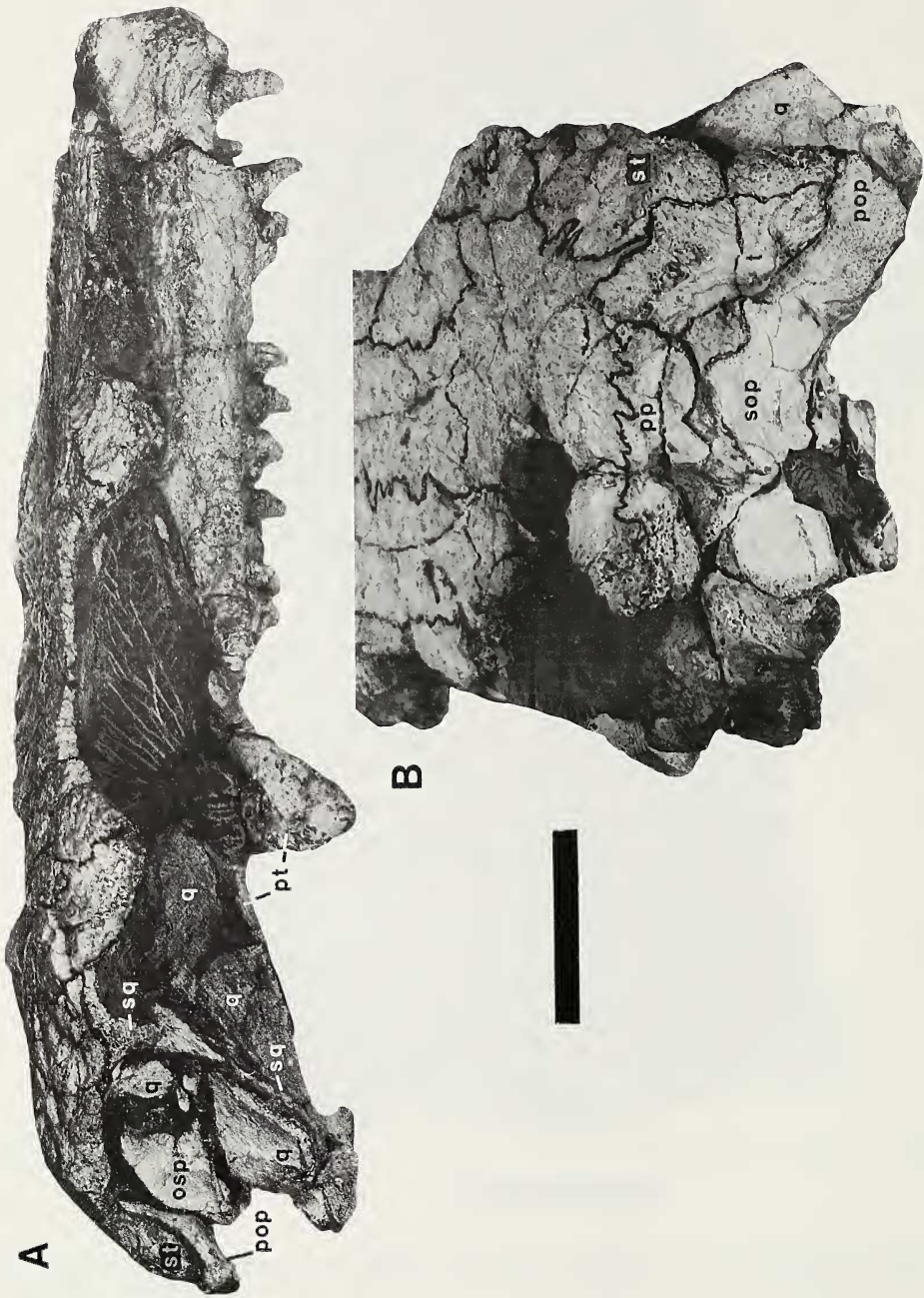
Fig. 9.—*Diadectes absitus*, paratype (MNG 8747). Skull in A, lateral and B, occipital views. Scale = 2 cm.

Fig. 10.—*Diadectes absitus*, paratype (MNG 8747). Skull in ventral view. Scale = 2 cm.

in MNG 8747 indicates clearly that the stapedial footplate articulates with the posterolateral region of its outer, convex surface.

In MNG 8747 the left exoccipital has been lost, revealing that it did not contribute to the articular surface of the condyle, but rather extended along its dorsal surface as a thin sheath flooring the foramen magnum. Immediately above its contact with the condyle the exoccipital is strongly waisted medially before continuing as a dorsomedially directed, wing-like process that borders the foramen magnum laterally. The exoccipital–opisthotic suture is quite distinct on the occiput, extending ventrolaterally onto the ventral margin of the braincase. Here it continues anteriorly, first intersecting the lateral margin of the large jugular foramen, presumably for cranial nerves IX–XI and the jugular vein, and then extends a short distance along the anteromedial basal margin of the otic trough before terminating. Although there is no visible supraoccipital–opisthotic suture, its approximate position, however, can be presumed. On the right lateral margin of the supraoccipital–opisthotic is a small opening bordered laterally by the tabular. This opening, visible on both sides in MNG 8853, is almost certainly the posttemporal fenestra, but is believed to be lost in very mature adults specimens (Berman et al., 1992). Typically in amniotes the supraoccipital–opisthotic suture extended dorsolaterally from the dorsolateral margin of the foramen magnum just above the contribution of the exoccipital to this opening and ended at or near the medial margin of the posttemporal fenestra. Immediately adjacent to and on either side of the foramen magnum in MNG 8747 is a shallow, 5 mm-long, horizontal groove occupying the presumed, approximate position of the proximal end of the supraoccipital–opisthotic contact.

Stapes. In MNG 8853 both stapes are present, but only the right is fully exposed (Fig. 5, 6, 7B), whereas in MNG 8747 only the right is present and exposed (Fig. 9A, 10). In general the stapes is divisible into two parts: an expansive, flat, distal plate that occupies the otic (or temporal) notch and a short proximal shaft with an expanded footplate. Because it could not be determined whether the distal plate represents an ossified tympanic membrane or is completely or partially stapedial, it was termed simply the "ossified plate" by Olson (1966). In MNG 8853 the ossified plate occupies nearly the entire otic notch, with its lateral perimeter reaching to within 3 or 4 mm and paralleling the otic notch. A short, stapedial shaft projects dorsomedially from the medial margin of the ossified plate at a level about one-fourth the distance down in its height. Below the shaft the dorsal two-thirds of the medial margin of the ossified plate thickens greatly and extends a short distance as it wraps around the medial margin of the quadrate. At the base of the shaft there is a small, hemispherical swelling of the ossified plate. The bluntly pointed ventral end of the ossified plate closely approaches the small, triangular, medial process of the quadratojugal at the posteroventral margin of the otic notch. In the juvenile MNG 8747 the precursor material of the ossified plate had apparently only partially ossified, and the plate occupies only the dorsal half of the otic notch. The dorsal, or posterodorsal, and ventral margins of the plate exhibit smoothly finished edges, whereas the anterior margin is incompletely preserved. The posteroventral corner of the ossified plate thickens as it continues into the medially directed stapedial shaft. The shaft is very short and has an anteroposteriorly elongated, suboval cross section. The footplate is subtriangular in ventral view, with the posteromedial corner being greatly elongated. The medially facing surface of the footplate is slightly concave, with an irregular, roughened surface that suggests it had a cartilage covering. It is reasonable to assume that this surface articulated with the posterolateral surface of the otic trough of the opisthotic, from which it is only very narrowly separated. A small stapedial foramen pierces the posteroventral surface of the shaft.

Mandible. The greater part of the right lower jaw of MNG 8747 is preserved and has been separated from the skull (Fig. 11). It is missing large portions of the splenial, angular, and prearticular that border the medial fenestra ventrally and posteriorly, and almost the entire articular. The left jaw is very incomplete, but importantly includes the symphyseal portions of the dentary and splenial, as well as the first four teeth and the roots of the fifth and sixth. This portion has also been separated from the skull (Fig. 11E), whereas a badly damaged midlength portion remains attached to the skull. Although the lower jaws of MNG 8853 are complete, their attachment to the skull allows only partial exposures of the lateral and medial surfaces. In MNG 8747 the cross-sectional shape of the jaw posterior to the symphyseal region is subcircular, with the mediolateral width being slightly greater than the dorsoventral depth at the level of the coronoid eminence. As a result, the adductor fossa faces almost directly dorsally, and the incompletely preserved medial fossa apparently faced primarily ventrally. This arrangement nearly prevents the two openings from being visible in a single orientation of the jaw. On the other hand, in MNG 8853 jaw depth very slightly exceeds the width at the same level, and both fossae are clearly visible in medial view. These differences almost certainly reflect different ontogenetic stages.

With the exception of proportions, the lower jaw of *D. absitus* specimens deviates in only a few minor ways from those of North American members of the genus. However, because the only detailed description of a lower jaw of *Diadectes* (Welles, 1941) was based on an imperfect specimen (UCMP 33903), it is necessary to comment on some aspects of its anatomy in *D. absitus*. In lateral view of
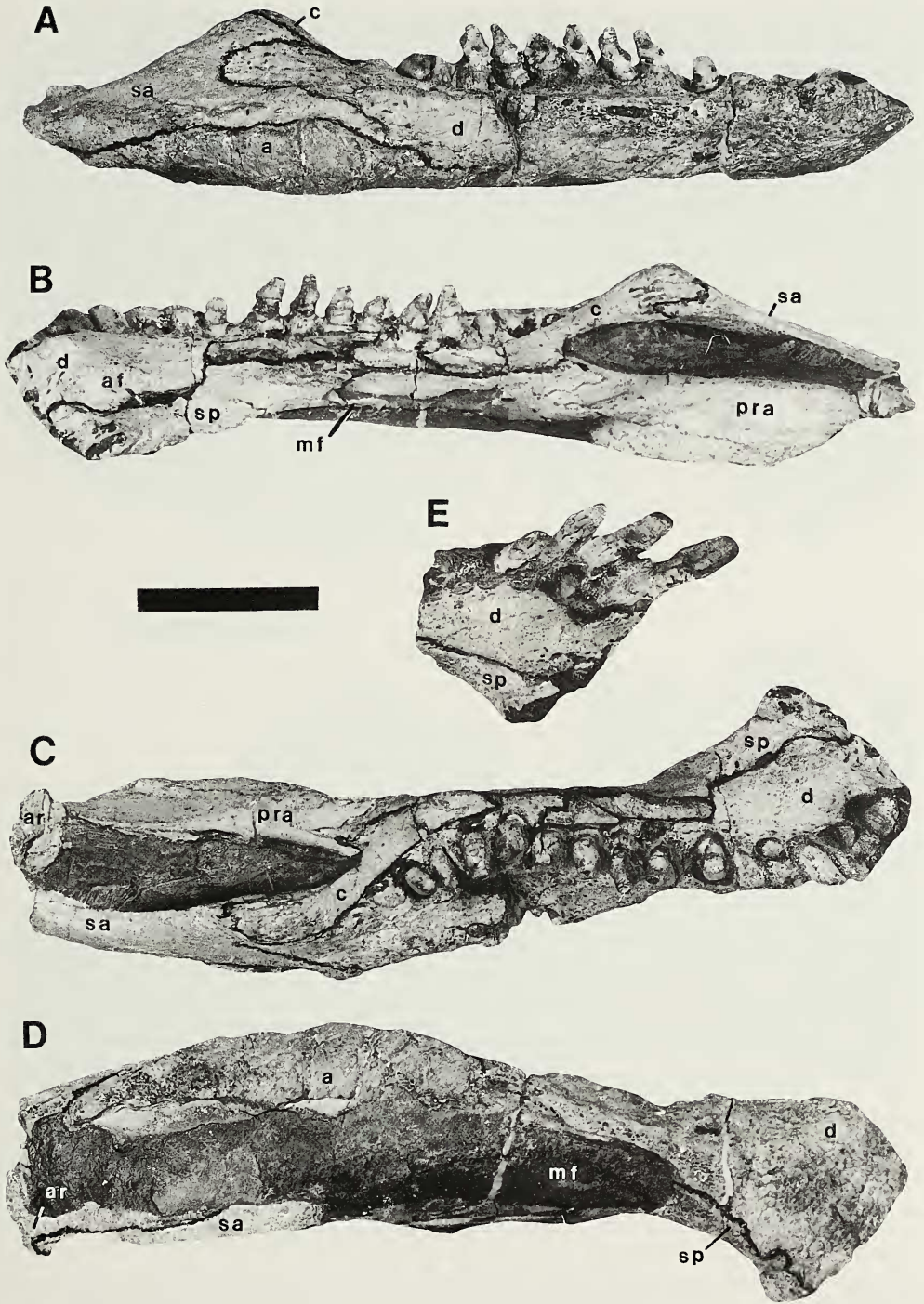
Fig. 11.—*Diadectes absitus*, paratype (MNG 8747). A–D. Right lower jaw in lateral, medial, dorsal, and ventrolateral views. E. Symphyseal region of left lower jaw in medial view. Scale = 2 cm.

the jaw the surangular tapers anteriorly along its dorsal contact with the angular as a wedge-shaped process to a level about one-fourth the distance back in the length of the angular (Fig. 11A). An unusual feature clearly visible in the right lower jaw of MNG 8747 is the formation by the dentary of a wide, dorsally facing platform lateral to the cheek teeth (Fig. 11C). This structure is also visible in the right lower jaw of MNG 8853; however, it appears to be relatively narrower and possibly bordered by a low, rounded facial ridge of the dentary.

The dentary dentition is exposed only in MNG 8747, and, as in the upper dentition, is typical of that in *Diadectes*. However, the reasons for giving the above brief account of the upper marginal dentition also apply here. The right dentary possesses 15 teeth, although only the bases of the first five, and the 13th and 15th remain; fortunately, the first four teeth of the symphyseal region of the left jaw are well preserved. The first three are distinctly procumbent and incisiform, decrease markedly in size posteriorly, are narrowly separated, and, as in the premaxillary teeth, are broadly concave on the distal portion of their lingual surface, giving them a chisel-like appearance in lateral view. The fourth tooth is smaller than the preceding tooth and intermediate in form between the anterior incisors and the succeeding molar-like teeth. The molar-like cheek teeth of the series increase in size posteriorly to the ninth or tenth, then decrease gradually to the 13th, with the last two decreasing markedly. Their degree of molar-like development clearly reflects a juvenile stage of growth (Berman and Sumida, 1995). The ninth tooth of the series measures 6.0 mm in transverse width, 3.0 mm in anteroposterior length, and 4.0 mm in estimated height (the crown is badly worn). Although transversely expanded, the labial sides of the teeth are positioned well in advance of the lingual sides. The lingual and labial cusps of the cheek teeth are poorly developed and perhaps would be more accurately described as "shoulders," whereas the subconical central cusps are well developed and account for about half the height of the crown. The lingual cusps appear to be more pronounced than those of the labial side, as the bases of the central cusps are more expanded labially than they are lingually.

The coronoid, which was absent in the *Diadectes* specimen described by Welles (1941), is well preserved and entirely exposed in the right jaw of MNG 8747 (Fig. 11A–C). The coronoid forms almost the entire coronoid eminence of the jaw, which attains a height slightly above the level of the cheek teeth. Although visible in both lateral and medial views of the jaw, the coronoid is more expansive medially and forms the anterolateral border of the adductor fossa. The coronoid eminence is much thicker transversely than the surangular portion of the adductor fossa rim. From the anterior corner of the adductor fossa the coronoid extends anteriorly as a mediolaterally flattened, narrow, rectangular plate that sheaths the medial surface of the alveolar shelf of the dentary while contacting the splenial and prearticular along its ventral margin. Anteriorly the coronoid extends to the level of the sixth maxillary tooth, although there is a small gap at about the level of the 11th tooth.

In ventral view of the mandible of MNG 8853 (Fig. 7A) the splenials are exposed in part as narrow bands extending posteriorly from the symphysis along the ventromedial margin of the jaw. At about their midlength they taper posteriorly to a sharply pointed process that penetrates the anterior end of the angular. This results in the splenial being separated from the ventral border of the medial fenestra by a narrow, marginal splint of angular. Just posterior to the symphysis on the medial surface of the right jaw of MNG 8747 the dentary–splenial suture opens narrowly for a few millimeters. The margins of the opening are smoothly rounded, giving it the appearance of a fenestra. Welles (1941) identified and referred to this opening in *Diadectes* as the anterior fenestra and described it as communicating with the Meckelian canal or, as he preferred, the primordial canal.

Axial Skeleton. The complete presacral column of MNG 8853 is visible for the most part in dorsal view (Fig. 1) and includes 21 vertebrae. The atlas–axis complex is complete, although the strong, lateral angulation of the skull to the left side of the vertebral column has resulted in the disarticulation between the atlantal intercentrum–neural arch and the fused atlantal pleurocentrum–axial intercentrum components (Fig. 12). In most of its key features the complex conforms closely with that in North American species (Sumida and Lombard, 1991). Both proatlases are exposed in dorsal view, but only the right one is well exposed and little distorted. Both contact the occiput adjacent to and at the midheight level of the foramen magnum, but it is uncertain that this represents their actual point of contact with the skull. They are disarticulated from and lie just lateral to their respective atlantal neural arch halves. The right proatlas, as seen in dorsal view, consists of two subequal parts: an expanded, subcircular anterior end from whose posterior margin projects a slightly tapering, spine-like process. The anterior expanded end is strongly inclined anterodorsally, so that its ventral surface, undoubtedly the site of an articulation facet, contacts the occiput of the skull. The spine-like posterior portion, the epipophysis, must have projected directly caudally. There is a ventral thickening at the base of the epipophysis, whose ventral surface presumably possesses a facet for articulation with the atlantal neural arch.

The atlantal neural arch halves are preserved in very nearly their correct orientation and articulation with one another, the atlantal intercentrum, and the occipital condyle of the skull. The upper halves
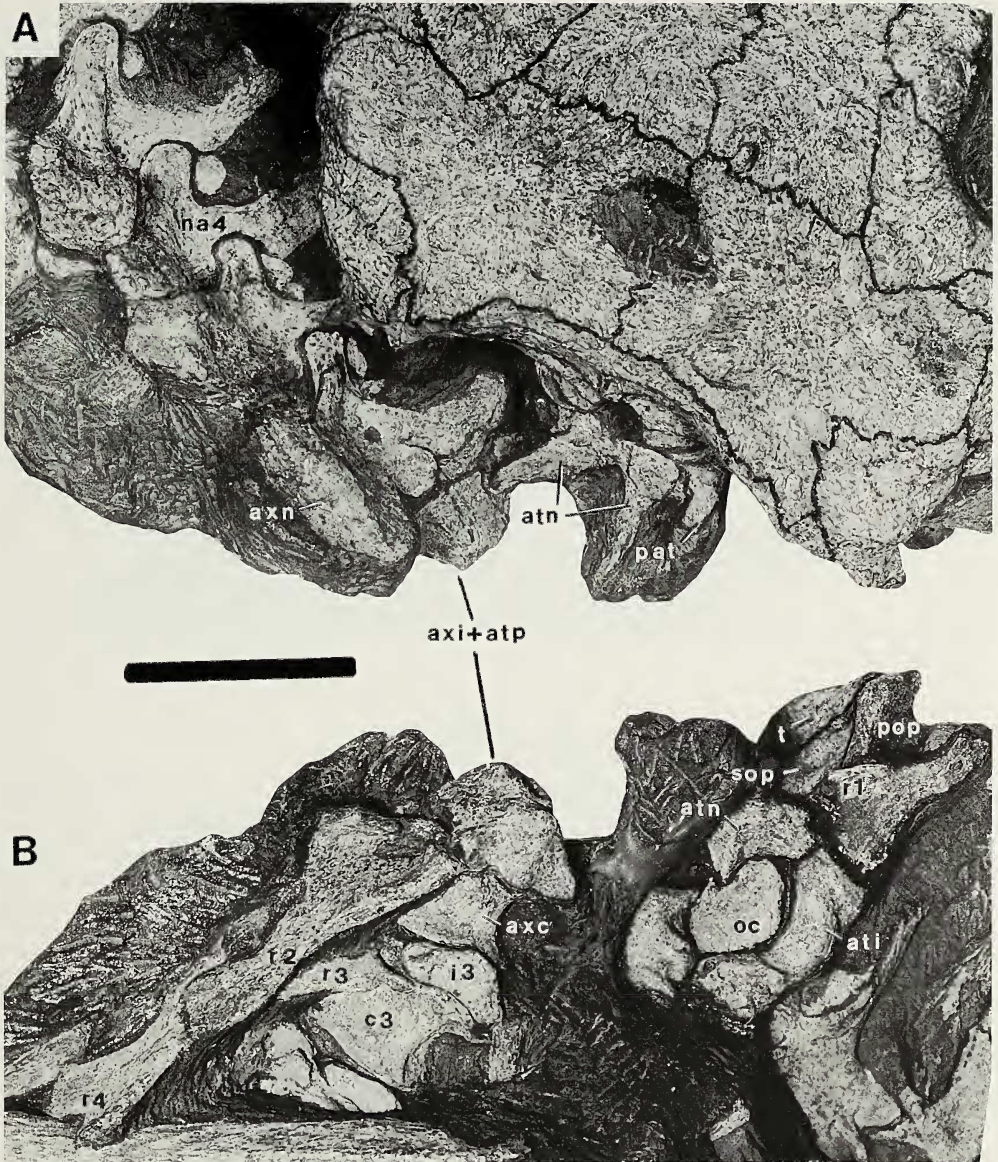
Fig. 12.—*Diadectes absitus*, holotype (MNG 8853). A. Posterior region of skull and first five cervical vertebrae in dorsal view. B. Same region as in A exposed on reverse side of block showing atlantal intercentrum and paired atlantal neural arches in posteromedial view, fused atlantal pleurocentrum and axial intercentrum in right ventrolateral view, central elements of cervical vertebrae 2–4 in ventral view, right atlantal rib in medial view, and right ribs 2–4 in lateral view. Scale = 3 cm.

of the arches are exposed in dorsal view and appear as a larger version of the proatlas. The dorsal surface of its rounded, anterior end is occupied almost entirely by a flat, anterior zygapophyseal facet for the proatlas. Medial to the facet there is a small, rectangular extension by which the arch half contacted its mate on the midline, whereas laterally (visible only on the right arch half) there is a very small triangular protuberance. Posteriorly the arch halves consist of a long, spine-like process which tapers to a sharp point and, as in the proatlas, is identified as an epipophysis. Posteriorly the

epiphyses diverge slightly from the midline. A ventral thickening at the base of the epiphysis buttresses the posterior zygapophysis. Below the level of the pre- and postzygapophyses the arch halves are visible only in posteromedial view (Fig. 12B). Each consists of a subrectangular plate with its long axis directed ventrolaterally and its internal surface facing strongly posteriorly and slightly ventromedially. The dorsomedial margins of the plates are slightly concave and diverge posterodorsally from the midsagittal plane, as they form the ventral half of the neural canal. The anterior margins clearly contacted the dorsolateral edges of the occipital condyle, whereas the ventral margins have a broad contact with the atlantal intercentrum. A short but vertically elongate diapophysis for the tuberculum of the atlantal rib projects ventrolaterally and slightly posteriorly from very low on the posterior margin of the lateral surface.

In posterior view (Fig. 12B) the atlantal intercentrum is in general crescent-shaped, with the apices of the dorsally directed lateral wings contacting the bases of the atlantal neural arches. The posterior face of the midcentral area is excavated into a broad, shallow concavity. The midventral length of the atlantal intercentrum is very short, perhaps only 2 mm. A short, vertically elongate parapophysis for the capitulum of the atlantal rib projects ventrolaterally from the lateral surface. The anterior rim of the atlantal intercentrum contacts the ventral half of the occipital condyle rim.

As previously described (Sumida and Lombard, 1991; Sumida et al., 1992) in North American *Diadectes*, the atlantal pleurocentrum in MNG 8853 is fused to the dorsal surface of the axial intercentrum. In lateral view (Fig. 12B) the pleurocentral portion has the appearance of a low, rectangular block. However, strong, laterally oblique crushing has resulted not only in some transverse narrowing of the element, but also in its right lateral surface facing ventrolaterally so as to be visible in ventral view of the complex. The flat dorsal surface of the centrum (Fig. 12A) is of unfinished bone except for a smooth, middorsal channel which ends just short of the anterior margin. The channel may represent the floor of the neural canal. These features suggest that the pleurocentrum was continued dorsally by cartilage that may have ossified later in ontogeny. In ventral view of the complex the intercentral portion has a subtriangular outline with the apex directed anteriorly and a very low, broadly rounded midline surface. The posterolateral corners are extended slightly and end in a truncated margin as the parapophyseal processes for the capitular head of the axial rib. The anteriorly directed apex is exaggerated slightly to form a bluntly rounded extension whose tip likely contacted the midventral concavity on the posterior surface of the atlantal intercentrum.

Exposure of the axis in MNG 8853 is limited to the left side of the neural arch and the right side of the centrum, and the two elements appear to be fused (Fig. 12). There is no swelling or lateral expansion of the arch, as in the immediately succeeding vertebrae. The blade-like neural spine is long and low, not exceeding the height of the more posterior spines, and thickens considerably toward its distal and posterior margins. Close to the posterior margin on the lateral surface of the spine is a well-developed, sharp-edged ridge that extends ventrally from the crest to the anterior edge of the base of the postzygapophseal buttress. The zygapophyses are set close to the midline, although the posterior set is slightly wider apart. Whereas the anterior zygapophyses and their facets are oval, the posterior set are narrowly subrectangular. Both sets of facets slope slightly ventrolaterally. The partially exposed centrum exhibits a moderately developed midventral keel.

In MNG 8853 the intercentrum of the third cervical (Fig. 12B) is about two-thirds the size of that of the axis and is weakly chevron-shaped with the apex directed anteriorly, as reported in *Diadectes* (Sumida and Lombard, 1991). Intercentrum 4 and those of succeeding vertebrae are much smaller and have a laterally expanded oval outline.

The postaxial neural spines (Fig. 1) are low and roughly diamond-shaped in horizontal section, with the long axis oriented anteroposteriorly. They increase slightly in transverse width from the third to the seventh vertebra, becoming nearly quadrangular in horizontal section, then decrease in width gradually in the succeeding seven or eight vertebrae to a narrow diamond outline that is essentially maintained to the end of the presacral series. The summits of the spines are very coarsely textured, giving them an irregular margin. This is particularly true of those in the anterior half of the presacral series, where the summits are slightly expanded, giving the spines a slightly mushroom-like appearance. Additionally, in this region of the column there is also a bilateral constriction of the neural spine close to the posterior corner of its summit, so that in dorsal view this angle of the spine is converted into a process-like structure. A further variation in spine structure is seen in the vertebrae near the posterior end of the dorsal series in MNG 7721, where the lateral, angular margins of the spines are expanded laterally into short, irregular processes (Fig. 1, 13C). One noticeable exception to the general structure of the postaxial dorsal neural spines given above is that of the fourth vertebra in MNG 8853 (Fig. 1, 12A), which is greatly reduced in both its lateral and longitudinal dimensions to a nearly blade-like structure (a similar condition is seen in the amphibian *Eryops*; Moulton, 1974). Seemingly, longitudinal compression of this region of the column has brought the neural spines of these three vertebrae into contact.
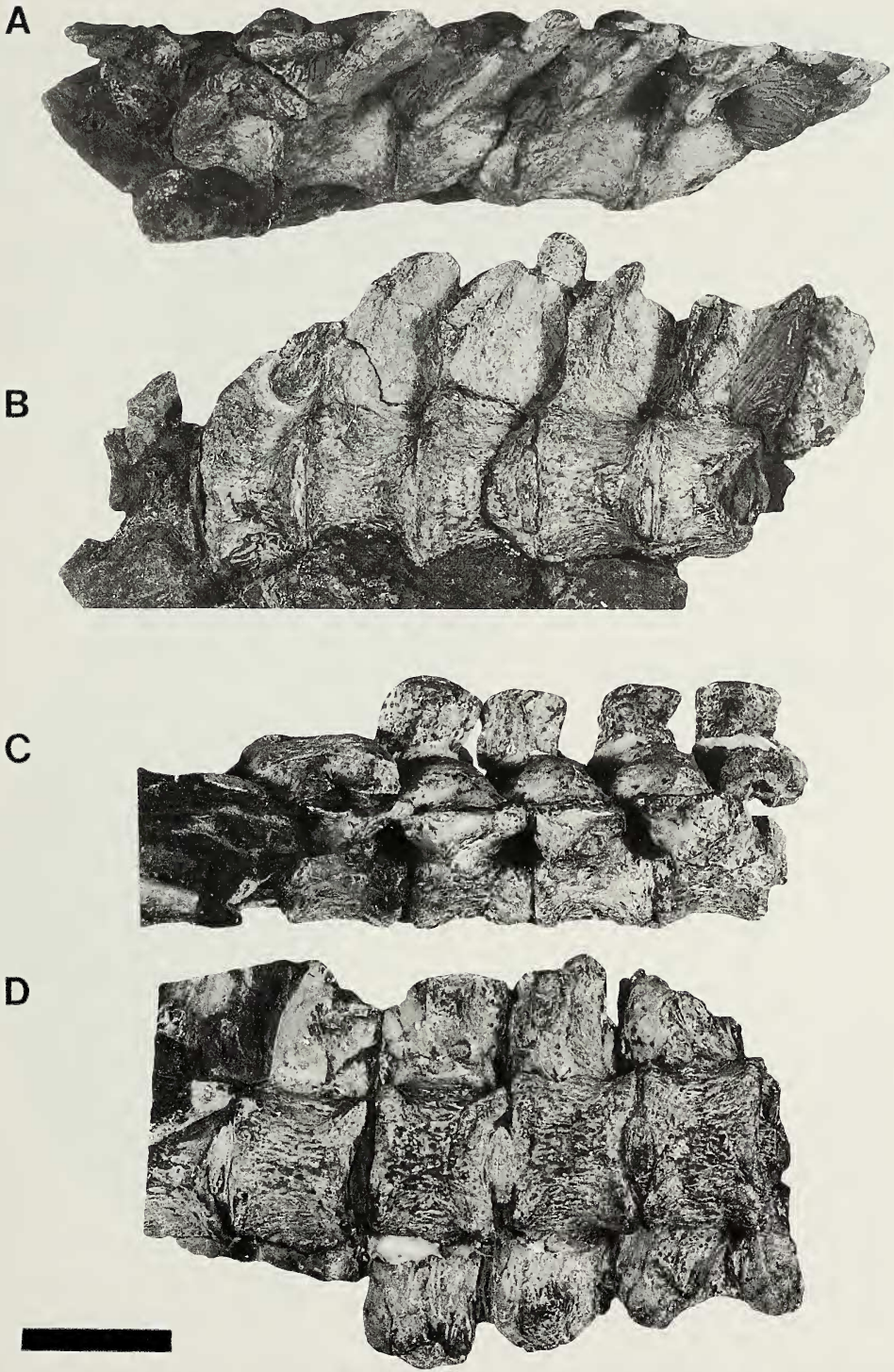
Fig. 13.—*Diadectes absitus*, paratype (MNG 7721). A, B, Postaxial cervical and C, D, posterior dorsal vertebrae in lateral and ventral views (anterior to the left), respectively. Scale = 4 cm.

The neural arches of all the presacrals of the postcervical region (Fig. 1) are swollen, with the zygapophyses extending laterally well beyond the lateral margins of the centra. In the first nine vertebrae there is a marked, successive increase in the lateral extent of the zygapophyses from very close to the midline in the atlas–axis complex to nearly equalling the lateral extent of the transverse processes. More posteriorly, the presacrals exhibit only a very gradual increase in this dimension. The low, squat structure of the presacrals is expressed particularly in the near-horizontal plane occupied by the dorsal crests of the posterior zygapophyseal buttresses. The zygapophyseal planes in the cervical region appear to slope slightly posteroventrally, whereas those of the rest of the presacrals are horizontal.

Lateral and ventral views of the presacral vertebrae have been possible only in two short series in MNG 7721 (Fig. 13): one includes five postaxial cervicals lacking mainly the neural spines and the other includes six dorsals (only five are shown) from just anterior to the sacrum. Their differences are reflected mainly in the structure of the transverse processes. In the vertebrae from the cervical region the transverse processes are laterally projecting, anteroposteriorly thin, and dorsoventrally elongate ridges. In lateral view they extend diagonally anteroventrally from the posterior surface of the anterior zygapophysis to the upper portion of the anterior centrum rim. The narrow costal facets for the ribs face ventrolaterally and slightly posteriorly and show no noticeable expansions demarking capitular and tubercular areas. In end view of the vertebrae the processes shorten gradually in lateral extent as they extend anteroventrally, but still end with a rather long, nearly horizontal ventral margin. The transverse processes in the string of posterior dorsals are thicker, project directly laterally, and are restricted to the posterior surface of the anterior zygapophyseal buttress and do not extend onto the centrum. Their wider costal facets face mainly laterally and slightly posteroventrally and are slightly constricted into nearly equal capitular and tubercular regions, the former being a little wider. Disarticulation of the last or sixth vertebra of the string of far posterior dorsals reveals the absence of hypantrum and hyposphene accessory articulations. The last two vertebrae of the string are deeply amphicoelous, but do not appear to be notochordal. In some of the vertebrae there is an indication of a neurocentral suture which may suggest a less than fully mature condition.

Except for the atlas–axis complex, the centra of the presacral vertebrae are spool-shaped, with horizontal diameters of the ends exceeding the lengths in the cervicals and farthest posterior presacrals in MNG 7721 by approximately 40 and 18%, respectively. The lateral surfaces of the centra are flared moderately outward to thickened, semicircular rim lips. Flaring of the ventral surface of the centrum is much less pronounced, and there are no midventral ridges. The midventral margin of the posterior rim of the centrum is bevelled to accommodate the small intercentrum.

All that can be seen of the two sacral vertebrae in MNG 8853 (Fig. 1) are the poorly preserved neural arches. However, a large portion of the tail of MNG 8853 is preserved (Fig. 1, 14) and includes a string of 18 vertebrae, although nine are represented only by intercentra or haemal arches. As preserved, the first five vertebrae of the series are represented by only the intercentra in dorsal view. They have a narrow, oval outline and are aligned as if retaining their original spacing and orientation. The caudal series is continued posteriorly by nine complete, laterally exposed vertebrae that diminish steadily in size posteriorly. Their neural arches are narrow, not swollen, with the zygapophyses positioned close to the midline. The anteriormost neural spine of the series curves slightly posteriorly and is blade-like for most of its length, as it terminates distally in a cap-like lateral expansion that is narrowly oval in dorsal view. More posteriorly the spines gradually straighten to a vertical orientation, decrease dramatically in size, and quickly reduce and lose the cap-like expansion at their distal end. The oval zygapophyseal planes slope steeply ventromedially. The transverse processes are exposed only in dorsal view and are positioned at about midheight on the centra and adjacent to the anterior central rim. They exhibit a marked, successive decrease in size posteriorly. In the anteriormost preserved neural arch, vertebra 6 of the series, the transverse process is rather broad and long, projects directly laterally, and narrows slightly distally along its posterior margin. By the posteriormost preserved neural arch, vertebra 14 of the series, the process is reduced to a very small, ventrolaterally projecting, triangular nubbin. The centra of this series are spool-shaped with moderately concave lateral surfaces. The lips of the central rims are laterally flared, but that of the posterior rim is far more pronounced. The ventral margins of the anterior central rims are strongly bevelled to accommodate the haemal arches. The small, proximal, intercentral portions of the haemal arches are narrowly rectangular in lateral view. As the long spines extend from the posteroventral corner of the intercentral portion they gradually double in anteroposterior width by their distal end.

Directly following the nine complete, articulated caudals the remaining, preserved portion of the tail ends in a series of four haemal arches that also retain their approximate spatial relationships and alignment with the preceding arches. Their dorsal and lateral surfaces are exposed, as well as the proximal portion of their posterior surface. Additionally, the entire posterior surface of a disarticulated haemal arch is exposed in MNG 7721. In posterior view the haemal arch is Y-shaped, with the

Fig. 14.—Incomplete tail of *Diadectes absitus*, holotype (MNG 8853; see also Fig. 1). Anteriormost and posteriormost vertebrae of series represented only by intercentra and haemal arches, respectively. Scale = 4 cm.

proximal, crescentic intercentral crosspiece spanning the ends of the two arms of the Y to enclose a triangular space. The roughened, posterodorsal articular surface of the intercentral crosspiece contacted the bevelled ventral rim of the centrum. The spine ends in a laterally flattened, blade-like structure.

An isolated string of four distal caudals with haemal arches is exposed in left lateral view a short distance to the right of the midlength region of the presacral column of MNG 8853 (Fig. 1). Their proximity to MNG 8853 and similarity to those of *Diadectes* leaves little doubt that they belong to this specimen. By way of comparison with Case's (1911) description of *Diadectes*, their serial placement is probably near caudal 25. The neural spines are very small, dorsally directed, and laterally flattened with truncated tips. The zygapophyses are set very close together, and their oval facets are inclined very steeply ventromedially. Transverse processes are absent. The lateral surfaces of the centra are moderately concave, and the ventral margin of the posterior rim is bevelled to accommodate the haemal arch. The haemal arches are shorter versions of those more anterior in the caudal series.

A complete set of presacral ribs is present and well preserved in MNG 8853 (Fig. 1), but a tightly overlapping arrangement permits adequate description of only those of the atlas and axis (Fig. 12B). The complete right atlantal rib is exposed in posterior or medial view and closely approximates its correct relationship with the atlantal neural arch and intercentrum. In this view the head and shaft, which are subequal in length, form a flat, planar surface. The broadly triangular rib head was probably dicephalous, as a weakly ossified region roughly defines a narrow gap between the well-developed capitulum and the much narrower tuberculum. The short shaft maintains a narrow width that curves slightly posteriorly to its transversely truncated distal end. The right axial rib is complete, exposed in anterior or lateral view, and nearly retains its proper association with the axis. It is essentially a larger version of the atlantal rib except for the gradual, distal expansion of the shaft to a width approximately 50% greater than its proximal end. There is a continued, progressive increase in the expansion of the rib shafts 3–7, with those of vertebrae 6 and 7 having a roughly banana-shaped outline. In the remaining presacral ribs only the dorsal margins of the tubercula are visible, and the shafts maintain a nearly constant, narrow width throughout their length. The shafts exhibit a gradual increase in length to about the 14th rib, then decrease to a length nearly equalling that of the atlantal rib. Whereas the first four ribs are only slightly curved, the succeeding rib shafts exhibit a moderate posterior curvature that becomes pronounced in the last four or five presacral ribs.

Shoulder Girdle. All the elements of the shoulder girdle are well represented except the interclavicle. In the holotype the right scapulocoracoid and cleithrum are exposed below the cervical region of the skeleton (Fig. 2, 15), whereas the right clavicle was found isolated above the cervical region and was subsequently removed (Fig. 16). In the paratypes MNG 7721 and 8778 only remnants of the articulated interclavicle, clavicles, and left scapulocoracoid are preserved (Fig. 16B).

The holotypic right cleithrum (Fig. 15) is complete, exposed in lateral view, and very nearly in its correct articulation along the anterior margin of the scapulocoracoid. The cleithrum of *Diadectes absitus* very closely duplicates that seen in North American specimens (Case, 1911; Romer, 1956). In lateral view it has a narrow, sickle-shaped appearance. The expanded, posterodorsally curving upper half of the element has separated slightly from the anterodorsal corner of the scapular blade, which it presumably overlapped laterally. The much narrower ventral stem of the cleithrum maintains a constant width as it extends ventrally, terminating at the level of the upper margin of the glenoid cavity.

As shown by the posterior view of the complete right holotypic clavicle (Fig. 16A), the stem and ventral plate meet in a sharply defined internal angle of 120°. The ventral plate is bowed ventrally, with much of the posterior portion turned upward abruptly into a high, transverse, vertical wall that quickly diminishes in height as it joins the dorsal stem. In ventral view (Fig. 16B) the ventral plate is narrow and triangular, and a smooth, narrowly triangular area of the posteromedial corner is depressed dorsally. The plate ends medially in a feathered edge. The narrow dorsal stem gradually tapers distally to a blunt point. A moderate, rounded ridge extends the entire length of the medial edge of the posterior surface of the stem. Lateral to the ridge the posterior surface of the stem forms a shallow channel that probably received the ventral stem of the cleithrum.

Although the right holotypic scapulocoracoid is complete, only the scapular blade and coracoid region anterior to the glenoid cavity are well exposed (Fig. 15). A suture cannot be found between the scapular blade and coracoid plate. The scapular blade is tall and narrow, and except for the weakly ossified, obliquely truncated anterodorsal corner, is subrectangular in outline. Most unusual, but typical of North American species (Romer, 1956), is the absence of a gradual, but pronounced posterior distal expansion of the blade. The full extent of the coracoid plate is clearly seen in MNG 7721 (Fig. 16B) by either remaining bone or lighter-colored, reduced areas of the matrix that indicate where bone had been present. The coracoid plate is strongly expanded anteroventrally into a smoothly curving, almost semicircular margin. The long, narrow glenoid cavity is essentially complete and extends directly to the posteriormost point on the margin of the scapulocoracoid. As is typical of early tetrapods, the glenoid is screw-shaped, facing posterolaterally and slightly ventrally at its anterior end and dorsally
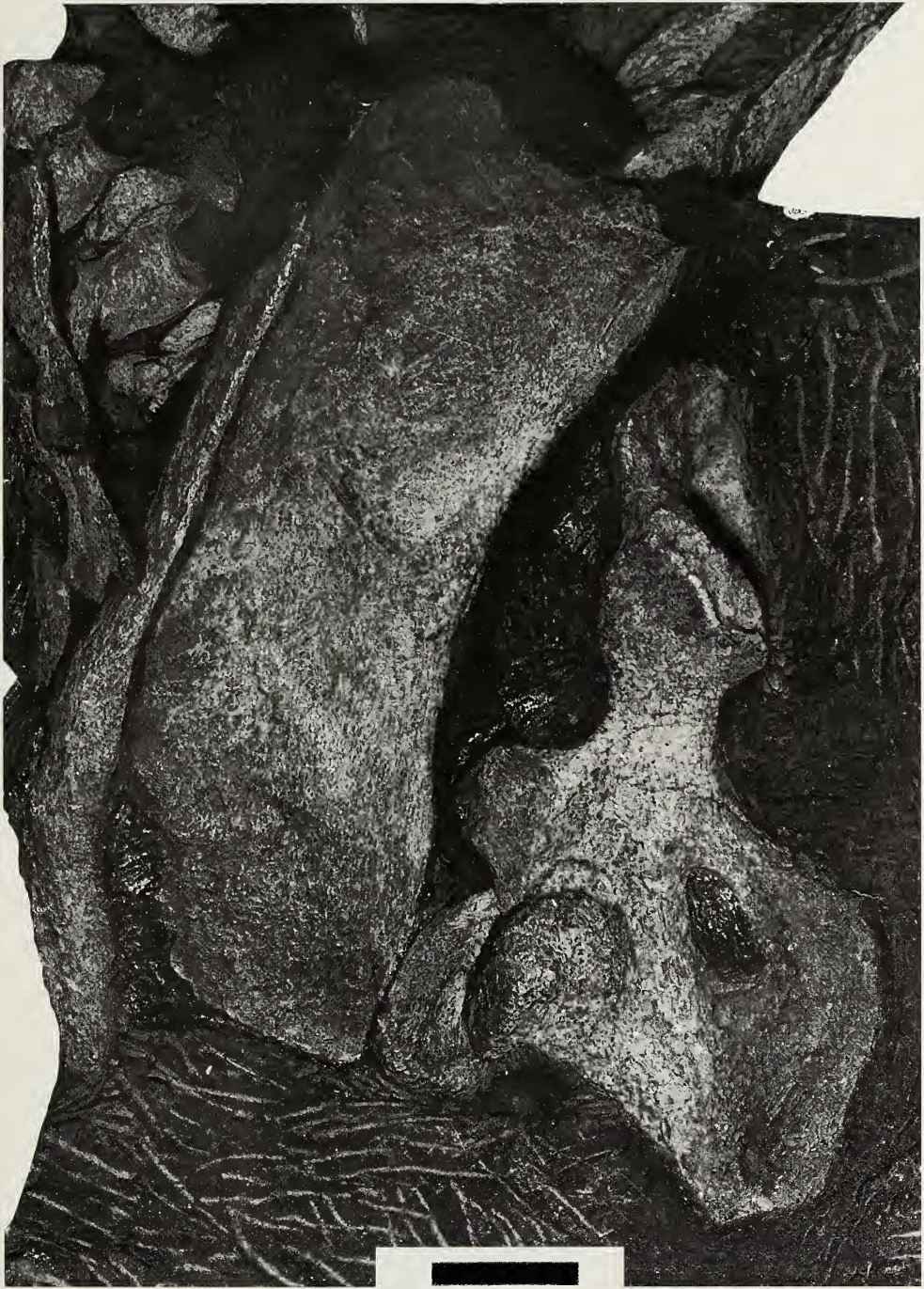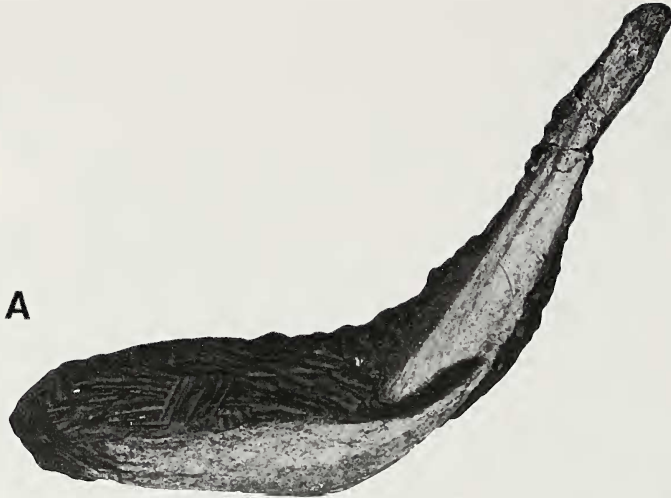
Fig. 15.—*Diadectes absitus*, holotype (MNG 8853). Right cleithrum and scapulocoracoid in lateral view (ventral margins toward top of page) and right humerus with distal expansion in ventral view (see also Fig. 2). Scale = 2 cm.

at its posterior end. A well-developed supraglenoid buttress supports the anterior end of the glenoid. Located beneath the anterior half of the glenoid is a partially preserved deep fossa. At the anterodorsal margin and deepest level of the fossa is a remnant of the coracoid foramen.

Forelimb and Manus. The humerus is best exemplified by the right element of the holotype MNG 8853 (Fig. 15), where it is exposed with the distal expansion in ventral view. The humerus has undergone some dorsoventral crushing and erosion of the surface bone. Because the humerus conforms very closely to those described (Case, 1911; Romer, 1956; Sumida, 1997) in North American *Diadectes*, only a few minor comparisons are required. The humerus of MNG 8853 appears to differ from that of the North American species in having 1) a slightly greater development of the crest of the proximal head for the attachment of the pectoralis muscle, 2) a greater distal expansion of the supinator process so that the angle formed between it and the capitellum is greater, 3) a more strongly distally hooked ectepicondyle, 4) a more transversely expanded trochlea, and 5) a slightly greater truncation of the posterodistal corner of the entepicondyle.

The only radius and ulna complete enough to warrant description are those articulated with the right manus in MNG 7721 (Fig. 17); an incomplete left epipodial pair is preserved in MNG 8978. Seen in dorsal (= anterior) view the radius has a relatively narrow, long shaft with moderately expanded ends. The proximal end is far more expanded than the distal end, and both expansions are slightly greater on the lateral margin of the bone. For most of its proximal length the cross-sectional outline of the radius is a mediolaterally expanded oval, with the medial margin flattened and the lateral margin drawn out into a narrowly pointed edge. This outline is continued to the concave proximal articular surface, whereas the poorly preserved distal end appears to have a subrectangular articular surface with the dorsoventral dimension being slightly greater.

The ulna is essentially complete in MNG 7721 except for the loss of the olecranon process. The complete bone may have been as much as 25% longer than the radius. What remains of the sigmoid notch is well defined. The bone is dorsoventrally (anteroposteriorly) narrow and greatly expanded mediolaterally. Because the ends are much more strongly flared medially than laterally, the medial margin is deeply concave. The dorsal surface of the distal end is very slightly convex. A dorsoventrally narrow articular surface, occupying the entire end of the bone, is partially divided by a shallow excavation on the ventral surface that approximates the distal margin angulation. Both distal facets face slightly ventrally, with that for the intermedium facing slightly medially and that for the ulnare facing slightly laterally.

The manus of MNG 7721 is nearly complete (Fig. 17), and the few incomplete elements, all phalanges, can be easily restored. The carpals are well articulated with no noticeable intervening spaces, suggesting a mature stage of development. The manus is exposed in dorsal view, but with the distal phalanges of digits 1–4 hyperflexed against the plantar surface. As far as known, this is the first complete carpus of *Diadectes* to be described, and it includes the expected elements, although there is no indication of a medial centrale or a pisiform ossification. The radiale is trapezoidal in outline and very thick, with a broad, flat proximal articular surface that appears to match that of the radius. The intermedium is subrectangular, but with a wedge-shaped medioproximal extension of the deep, oval ulnar articular margin. The oval ulnare is the dominant element of the carpus. Dorsal expansion of the proximal and distal margins produces a shallow, depressed central area. The lateral or proximal centrale is pentagonal in outline, with substantial contacts with the intermedium, ulnare, and distal carpals 2–4, and its proximomedial corner contacts narrowly the radiale. A series of five distal carpals is clearly defined. Distal carpal 1 appears as a small, equilateral triangle in outline and may have been displaced slightly laterally on its contact with the first metacarpal. The second distal carpal is a narrow, proximodistally elongated oval with the proximal end being wedge-shaped. Because distal carpal 2 contacts not only nearly the entire medial margin of the lateral centrale, but also the distolateral corner of the radiale, it is suspected that it may also include or has expanded to exclude the medial centrale. Distal carpal 3 is small and trapezoidal in outline. Distal carpal 4 is basically pentagonal in outline, with a proximal angulation that wedges partially between the medial centrale and the ulnare and a broad distal margin contact with metacarpal 4. The medial angulation of the fourth distal carpal contacts the lateral centrale and the third distal carpal, and its narrow, truncated lateral margin contacts the fifth distal carpal. The small, distal carpal 5 is a proximodistally short, lens-shaped element. An unidentified, subcircular element about 8 mm in maximum diameter and partially visible between

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Fig. 16.—*Diadectes absitus*. A, B. Right clavicle of holotype MNG 8853 in posterior and ventral views. C. Incomplete left scapulocoracoid of paratype MNG 7721 in lateral view (missing portions of bone indicated by reduced matrix). Scale = 2 cm.
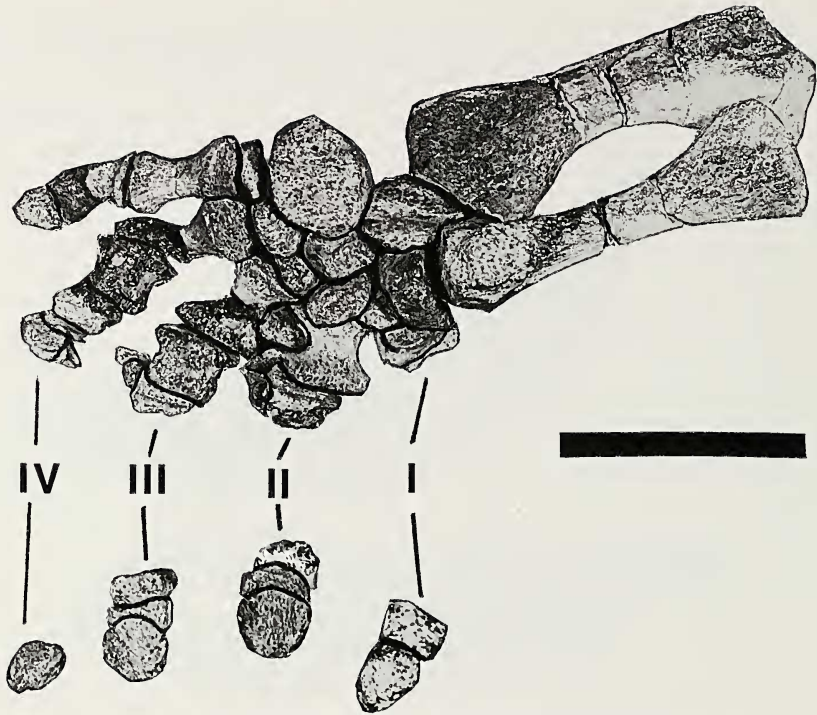
Fig. 17.—*Diadectes absitus*, paratype (MNG 7721). Articulated right radius, ulna, and manus in dorsal view. Distal phalanges of digits 1–4 are hyperflexed against plantar surface of manus and shown separately. Scale = 4 cm.

metacarpals 2 and 3 is suggestive of a carpal. Of the two carpal elements not accounted for in MNG 7721, however, a pisiform seems the most likely identification, as the tightly articulated carpus could not have accommodated a medial centrale.

Metacarpal 1 is very short and squat, whereas 2–5 are substantially larger and exhibit a gradual lengthening and narrowing serially. With two exceptions all five digits of MNG 7721 are well represented. The two phalanges of the first digit were lost due to weathering and were restored using their enclosing matrix as a natural mold to cast them in epoxy. Secondly, incomplete preservation makes it impossible to determine whether the fifth digit consisted of two or three phalanges. The phalangeal formula is, therefore, 2–3–4–5–2 or 3, but the higher count is suspected to be correct, as it is the usual formula of late Paleozoic terrestrial vertebrates. As is typical in *Diadectes*, all of the phalanges are short and broad, with the terminal ones ending in a bluntly rounded margin. An unusual *Diadectes* feature that is also present in MNG 7721 is the extreme proximodistal compression of the penultimate phalanges of digits 2–4.

Pelvis. The holotypic pelvis MNG 8853 is complete, although the ilia have suffered severe enough crushing to prevent detailed description (Fig. 1, 2, 18A). However, in MNG 8978 the disarticulated right ilium is complete and well exposed in lateral view (Fig. 18B). The anterior margin of the iliac blade is nearly vertical, with only a very slight anterodistal curvature. The posterior margin, however, is drawn out into a short, broadly triangular process that ends only a very short distance beyond the level of the expanded base of the ilium. There is no indication of an external iliac shelf, although such a structure is visible but poorly defined in the holotype. The long, quadrangular holotypic puboischiatic plate is well preserved and exposed in ventral view, with its lateral halves sloping ventromedially slightly to their midventral union to form to a modest keel. The plate is strongly waisted by the semicircular ventral rims of the acetabula, which occupy 44% of the plate's length. The union of the pubis and ischium cannot be detected, but is assumed to have occupied its normal position at about the midlength level of the acetabulum. If this is correct, the ischium is about twice the length of the pubis. Whereas the paired pubes end anteriorly in a low, triangular margin, the slightly convex posterior margins of the paired ischia form a wide, V-shaped notch in the plate. The anteroposteriorly
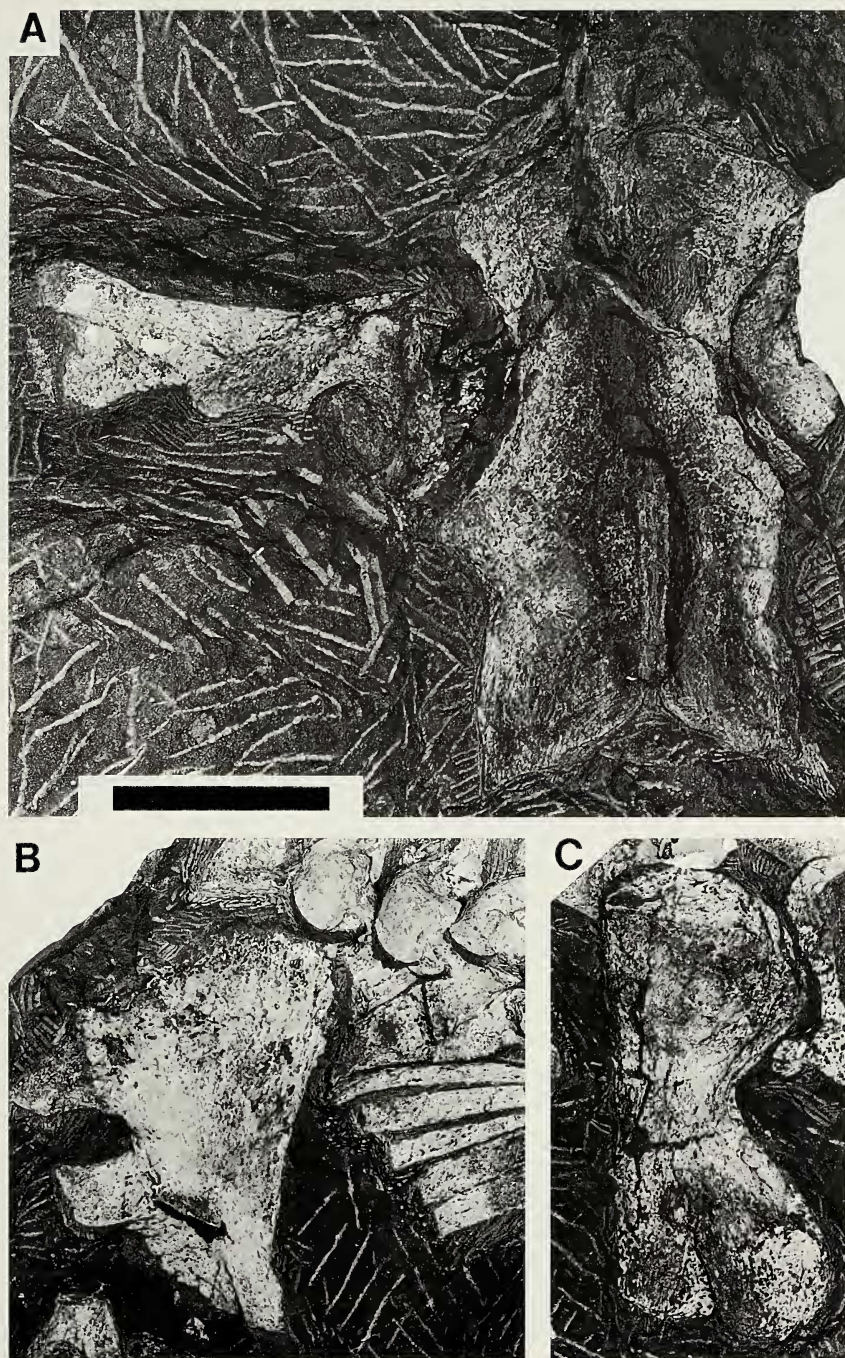
Fig. 18.—*Diadectes absitus*. A. Puboischiatic plate and femur of holotype MNG 8853 in ventral view (see also Fig. 2). B, C. Lateral view of right ilium and dorsal view of left femur of paratype MNG 8978. Scale = 4 cm.
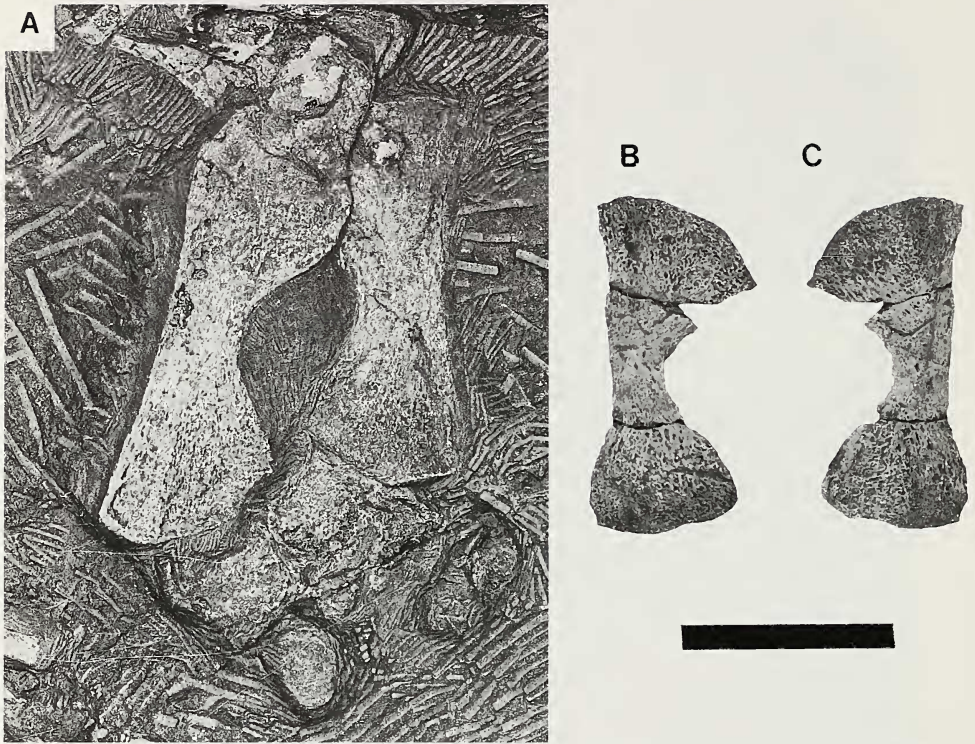
Fig. 19.—*Diadectes absitus.* A. Right tibia, fibula, and proximal portion of pes of holotype MNG 8853 in dorsal view (see also Fig. 1). B, C. Isolated left fibula of paratype MNG 7721 in dorsal and ventral views (distal end toward top of page). Scale = 4 cm.

elongate obturator foramina, defined by poorly preserved margins, lie midway between the antero-ventral margin of the acetabulum and the midventral union of the pubes.

Hindlimb and Pes. Femora are best preserved in the holotype MNG 8853 and MNG 8978, where the right of the former and the left of the latter are exposed in ventral and dorsal views (Fig. 18A, C), respectively. Both femora are complete, but the ends of MNG 8853 are not entirely exposed and those of MNG 8978 have been severely crushed dorsoventrally. The heads are widely expanded, subequal in length, and joined by a very short shaft in MNG 8853. In the smaller MNG 8978, however, there appears to be no intervening shaft. Dorsal view of the femur MNG 8978 shows the proximal and distal heads as angled posteriorly, so that the anterior margin of the bone is straight or slightly concave and the posterior margin is strongly waisted. The dorsal surface of the proximal head is broadly convex, and the narrow, terminal articular surface has a slightly crescentic outline, convex above, that thins more gradually posteriorly. As is customary, of the two distal condyles the posterior one is larger and extends a short distance farther distally. On the ventral surface of the femur MNG 8853 the depth of the intertrochanteric fossa is exaggerated along its anterior margin by a well-developed internal trochanter. The internal trochanter is continued to the distal corner of the fossa and onto to the shaft, where it becomes much more pronounced as the fourth trochanter.

The best examples of the tibia and fibula are the right elements in the holotype MNG 8853 (Fig. 19A), exposed in dorsal (= anterior) view, and an isolated left fibula in MNG 7721 (Fig. 19B, C). Although other examples of these elements are present in MNG 7721 and 8978, they are too poorly preserved to be informative. Both elements in the holotype are strongly crushed dorsoventrally (= anteroposteriorly), and most of the lateral half of the proximal head of the tibia is hidden by the overlying fibula. The fibula exceeds the tibia in length by 7%. Because the ends of the tibia are much more flared laterally than medially, the lateral margin of the bone is deeply concave, whereas the medial margin is only slightly concave. Despite the extreme crushing, the cnemial crest can be seen to end proximally in a prominent, knob-like rugosity. The heads of the fibula are much more greatly

expanded medially than laterally, so that, whereas the lateral margin of the bone is only slightly concave, the medial margin is strongly concave with essentially no separation of the heads by a shaft. The proximal head terminates in a very slightly convex margin that is directed slightly posteromedially (= dorsomedially), whereas the moderately convex margin of the distal head is oriented slightly anteromedially (= ventromedially). As seen in MNG 7721, a very low ridge on both the dorsal and ventral surfaces of the distal head lies close to and parallel with the lateral margin. The ventral surfaces of both heads are broadly concave. The proximal articular surface is crescentic in outline, with the concave margin ventral, and narrows slightly from a thicker, bluntly rounded lateral margin. The distal articular surface is weakly sigmoidal, with a slight constriction dividing it into a thicker, ventrally convex medial portion for the astragulus and a thinner, dorsally convex lateral portion for the astragulus and calcaneum.

Although elements of the pes are present in the holotype MNG 8853 (Fig. 1, 19A) and MNG 7721, they are so jumbled and poorly preserved that they are of little descriptive value. The dorsal (= anterior) surface of the astragulus is, however, clearly visible in MNG 7721 (not figured) and exhibits the standard L-shaped outline. The dominant, subrectangular horizontal limb occupies about 80% of the proximodistal length of the astragulus and exceeds by 2.4 times the mediolateral width of the much smaller neck. The rectangular outline of the neck is altered by a broadly rounded proximolateral corner for contact with the fibula. At the distal end of the lateral margin opposing the calcaneum is a small, semicircular notch of the perforating foramen. A channel-like depression extends proximo-medially from the foramen to the posteromedial angle of the astragulus. Just distal to the foramen the distolateral corner of the astragalus is beveled for contact with the fourth distal tarsal.

COMPARISONS AND DISCUSSION

European Diadectids

Of the vertebrates described from the Lower Permian of central Europe, only two genera can be assigned to Diadectidae with confidence, and both are from the Lower Rotliegend of Germany. On the basis of a string of six vertebrae that includes the last four presacral and two sacrals from the Leukersdorf Formation of the Erzgebirge Basin near Zwickau, Meyer (1860) described *Phanerosaurus naumanni*. The vertebrae are very much like those of *Diadectes*, having very broad, massive neural arches with far laterally placed zygapophyses. A second probable diadectid was described by Geinitz and Deichmueller (1882) from Nied-erhaeslich near Dresden in the Doehlen Basin. They described the disarticulated remains of what they believed to be two specimens representing a new species of *Phanerosaurus*, *P. pugnax*, preserved on a series of part and counterpart slabs. These remains were more thoroughly redescribed by Stappenbeck (1905), who concluded that they belonged to only one individual. On the basis of what he interpreted as differences in their vertebrae from those of *P. naumanni*, *P. pugnax* was reassigned to a new genus, *Stephanospondylus*, and both genera were placed in the new family Stephanospondylidae. Stappenbeck's description of *S. pugnax*, which included a reconstruction of both the skull and postcranium, was strongly criticized by Romer (1925). Romer convincingly demonstrated that the remains assigned to *S. pugnax* belong to two distinct forms, a diadectid closely allied to *Diadectes* and a labyrinthodont amphibian, possibly *Onchiodon*. Those elements recognized as belonging to *S. pugnax* include upper and lower tooth-bearing jaw elements, a squamosal and articulated parietals and frontals, presacral vertebrae, expanded ribs of the subscapular region, and elements of the pectoral girdle and forelimb.

If, according to Romer (1925:458), *Stephanospondylus* is defined by the above reduced list of elements, it "emerges as a typical diadectid, differing markedly in no known character from the well-known American forms, although a more com-plete knowledge of the animal might show differences to be present." Stappen-beck (1905) presented a list of seven vertebral characters for distinguishing be-

tween *Phanerosaurus* and *Stephanospondylus* and on this basis established the latter genus for *P. pugnax*. Romer (1925) regarded these characters, however, as either trivial, erroneous, or of uncertain value and, therefore, as providing little basis for recognizing two genera. Again, he cautioned that the discovery of additional remains of *Phanerosaurus* may indicate its distinctiveness. Therefore, Romer recommended that the genus *Stephanospondylus* be retained for the present and, although difficult to define, offered the following characterization (p. 459): ". . .a small diadectid, probably about 1 meter in length, lacking a hyposphene–hypantrum articulation; the subscapular ribs, although very broad, lack the V-shaped posterior angles found in *Diadectes*; the molar teeth lack lateral cusps." The potential usefulness of this diagnosis would possibly be even further diminished if it were determined that the holotype was a juvenile specimen. The secondary vertebral articulations and the greater development of the subscapular ribs may only appear in larger, more adult individuals, where structural support is more critical; both these structures also appear to be absent in the smaller Bromacker *Diadectes*. The absence of lateral cusps on the molar-like cheek teeth in *Stephanospondylus* could also be explained as a juvenile feature. Berman and Sumida (1995) have shown that in early juvenile stages of growth the cheek teeth in *Diadectes* are bulbous and lack lateral cusps. Although weakly developed, lateral cusps are, however, present in the juvenile Bromacker *Diadectes* skull MNG 8747. Yet, the length of this skull (ca. 100 mm) is far less than that of *Stephanospondylus pugnax*, estimated by Romer (1925) on the basis of the jaw elements to be about 155 mm.

There is one other piece of evidence to suggest that *Stephanospondylus* and the Bromacker diadectid are distinct forms. In addition to the tooth-bearing jaw elements, Geinitz and Deichmueller (1882) also figured the squamosal and the articulated parietals and frontals, which were used by Stappenbeck (1905) in his reconstruction of the skull of *S. pugnax*. These elements were also suspected by Romer (1925) to belong to *S. pugnax*. The surface ornamentation on each of the parietals and frontals, however, consists of narrow ridges radiating out from a central growth region. This pattern is most like that seen in typical labyrinthodonts and quite distinct from the network of pronounced, deep, smooth, U-shaped grooves superimposed on a coarsely granular or sponge-like textured sculpturing exhibited by the skull roofing bones in *Diadectes* (Olson, 1950; Berman et al., 1992), including the Bromacker skulls. In the absence of more complete materials *Phanerosaurus* and *Stephanospondylus* should be considered as very poorly defined, although they obviously share certain features with *Diadectes*. In fact, it is suspected that further examination of the known specimens would indicate that both genera should be considered as nomina dubia.

North American *Diadectes*

Although there can be no doubt of the generic assignment of the Bromacker diadectid to *Diadectes*, certain problems arise when attempting to compare it to North American representatives of the genus. In a study of the systematics of Diadectidae, Olson (1947) reduced significantly the number of recognized *Diadectes* species to three, possibly four, even after synonymizing several genera with this genus. Despite a marked reduction in the number of recognized *Diadectes* species, the basis for distinguishing between the remaining North American forms relies almost entirely on the extremely questionable grounds of size, proportions,

and stratigraphic position. Further complicating the systematics of this genus are Olson's (1947, 1950) observations that individual variations within a species are often greater than those between species, the tracing of sutures of the skull roofing bones is often difficult or impossible, and proportional differences are probably often the result of differential growth rates. The lack of detailed descriptions of early growth stages of both the skull and postcranium is particularly troublesome in recognizing differences between North American species of *Diadectes* (Olson, 1947; Berman et al., 1992; Berman and Sumida, 1995). Undoubtedly due in part to these problems, the numerous descriptions and reconstructions of the skulls of North American specimens (Huene, 1913; Gregory, 1946; Olson, 1947, 1950; Watson, 1954; Lewis and Vaughn, 1965) differ strikingly and contain serious errors in interpretation (Olson, 1947; Berman et al., 1992).

Despite the above difficulties, several autapomorphic and plesiomorphic cranial characters can be recognized that distinguish *Diadectes absitus* from all North American members of the genus. Polarities have been determined using the seymouriamorph *Seymouria* and anthracosaurs as the reference outgroups for comparisons, which follows most recent studies that recognize them as the closest outgroups to the diadectomorphs (Gauthier et al., 1988; Panchen and Smithson, 1988; Berman et al., 1992; Laurin and Reisz, 1995). Most recently, however, Carroll (1995) and Laurin and Reisz (1997) have presented a radically new scheme of tetrapod relationships which recognizes the lepospondyls as the nearest outgroup of the diadectomorphs and amniotes. Because of the narrow scope of relationship being tested and of the charcters being analyzed here, the alternative choice of lepospondyls as the nearest outgroup to diadectomorphs produces either ambiguous, the same, or no results. Because the Late Pennsylvanian diadectid *Desmatodon* is regarded to be a closely related predecessor of *Diadectes* (Vaughn, 1969, 1972; Berman and Sumida, 1995), it has also been included as a reference outgroup.

Dorsal Process of Premaxilla.—In *D. absitus* the dorsal process of the premaxilla is long and narrow, and extends a considerable distance onto the dorsal surface of the skull, reaching a level just beyond the posterior margin of the external naris. In all the reconstructions of North American *Diadectes* but that presented by Gregory (1946), the premaxilla is depicted as lacking a pronounced dorsal process. The presence of a well-developed dorsal process in the more primitive *Desmatodon* (Berman and Sumida, 1995), as well as in *Seymouria*, suggests that this is a plesiomorphic feature of *D. absitus*.

Anterior Extent of Prefrontal.—The prefrontal in *D. absitus* extends well beyond the level of the anterior margin of the frontal, whereas in North American *Diadectes* the prefrontal and frontal end anteriorly at approximately the same level. Inasmuch as a prefrontal extending beyond the anterior margin of the frontal is also seen in *Seymouria* and anthracosaurs, this feature is considered as plesiomorphic in *D. absitus*.

Shape of Postfrontal.—The postfrontal of *D. absitus* is chevron-shaped, with its posterior apex penetrating deeply into the anterior margin of the parietal. This configuration is due in part to a greater lateral extension of the postfrontal along the posterior margin of the orbit. In contrast, this element in North American *Diadectes* is generally subrectangular except for a lateral incisment by the orbital rim and has a straight or slightly posteriorly convex line of contact with the parietal. As the shape of the postfrontal in *D. absitus* is not seen in other late Paleozoic tetrapods, its presence in *D. absitus* is judged an autapomorphy.

Shape of Postorbital.—Typically the postorbital in North American *Diadectes* is shown as having a subrectangular outline, with a broad entrance into the orbit and a broad contact with the supratemporal. In *D. absitus*, however, the postorbital has a very narrow entrance into the orbit (due partly to the encroachment of the postfrontal) and forms for most of its posterior extent a tapering, triangular process that ends in a narrow contact with the supratemporal. By way of comparison with other late Paleozoic primitive tetrapods, the restricted entrance of the postorbital is considered an autapomorphic feature in *D. absitus*, whereas its posteriorly narrowing, triangular shape is judged as plesiomorphic. In view of the fact that early tetrapods lack a postorbital–supratemporal contact, the narrow contact of these two elements in *D. absitus* is judged a plesiomorphic character relative to the broad contact in North American representatives of this genus.

Ventral Margin of Jugal.—The abrupt, dorsalward, step-like retreat of the anterior portion of the jugal's contribution to the ventral margin of the skull in *D. absitus* is considered an autapomorphic feature. Among late Paleozoic tetrapods the ventral margin of the jugal either arches smoothly anterodorsally, as in North American species of *Diadectes*, or is straight.

Basicranial Joint.—The basicranial joint in anthracosaurs, *Seymouria*, *Desmatodon*, and immature specimens of North American *Diadectes* is obviously open and mobile, whereas in mature North American specimens of *Diadectes* the joint is firmly fused (Olson, 1947; Vaughn, 1972; Berman and Sumida, 1995). Although it is not unexpected that the basicranial joint is open and mobile in the juvenile specimen of *D. absitus* (MNG 8747), the retention of this feature in the adult Bromacker specimen (MNG 8853) can only be considered as a plesiomorphic state.

Cross-sectional Shape of Lower Jaw.—In *D. absitus* the lower jaw is subcircular in cross section for much of its length. At the level of the coronoid eminence in MNG 8747 the mediolateral width of the lower jaw is slightly greater than the dorsoventral depth, whereas in MNG 8853 the reverse is true. In contrast, the lower jaws of North American *Diadectes* are extraordinary for their exaggerated vertical expansion not only at the level of the coronoid eminence, but throughout almost their entire length. As examples, the lower jaws of *D. sanmiguelensis* (MCZ 2989), *D. lentus* (FMNH UC 675), *D. lentus* (UCMP 33903), and *Diadectes* sp. (UCMP 59023), which have lengths of 8.8, 13.2, 16.0, and 25.5 cm, respectively, the depth exceeds the width by about 2.7 times at the level of the coronoid eminence. The value for this ratio for the lower jaw of *Desmatodon hesperis* (CM 47670), measuring 12.0 cm in length, is about 1:2.2 and, therefore, more closely approaches the value for North American *Diadectes* than *D. absitus*. In anthracosaurs (Panchen, 1970) the depth-to-width ratio at the level of the coronoid eminence undoubtedly approaches that in North American species of *Diadectes*, although rough estimates of the value of this ratio in *Seymouria sanjuanensis* specimens CM 28596, 28597, and 38022 is only about 2.0. This survey suggests that the relatively low, approximately 1:1 depth-to-width ratio of the lower jaw in *D. absitus* should be judged as an autapomorphic character.

Labial Parapet in Lower Jaw.–In North American species of *Diadectes*, including early growth stages, and at least mature specimens of *Desmatodon*, there is lateral to the bases of the cheek teeth a shallow groove whose outer wall is formed by a vertical extension of the lateral surface of the dentary into a low, thin ridge or labial parapet (Welles, 1941; Lewis and Vaughn, 1965; Berman and Sumida, 1995). Among Paleozoic tetrapods a labial parapet of the dentary is

unique to the North American diadectids *Diadectes* and *Desmatodon*. Although the lower jaws of both the juvenile and adult *D. absitus* specimens MNG 8747 and 8853 lack a labial parapet of the dentary, they possess in its place the equally unique feature of a wide, flat, dorsally facing platform lateral to the cheek teeth. Because of the likelihood that these two features are functionally related, the combined characters of an absence of a labial parapet and the presence of a wide, dorsally facing labial platform is judged an autapomorphy of *D. absitus*.

The above combination of autapomorphic and plesiomorphic characters of *Diatectes absitus* provides a much broader basis for defining this species than is available for distinguishing between those of North America. The greater uniqueness of *D. absitus* may reflect its wide geographic separation from the North American species. On the other hand, its greater primitiveness reinforces the assessment, reached previously on the basis of the character of the entire Bromacker assemblage (Berman and Martens, 1993; Sumida et al., 1996), that the biostratigraphic position and age of the Tambach Formation, lowermost formational unit of the Upper Rotliegend, should be considered earliest Permian Wolfcampian.

Contradictory Descriptions

There exist at least two sources of important, misleading information about the anatomy of the North American species of *Diadectes* that contradict the description given here for *D. absitus*. In a recent redescription by Berman et al. (1992) of the skull of North American *Diadectes*, based almost entirely on a single specimen (CM 25741), the temporal region was misinterpreted. Most importantly, in their description the supratemporal was mistakenly interpreted to have an extensive, medially directed occipital expansion that contacted broadly the lateral and posterior margins of the postparietal as it extended to within a short distance of the skull midline. Further, whereas the supratemporal was correctly shown as forming almost the entire posterolateral, horn-like extension of the skull table, the tabular was incorrectly shown as a very small element occupying a position medial to the distal end of the skull table extension and as incorporated into the occipital plate. This sutural pattern, considered an autapomorphy of *Diadectes* (Berman et al., 1992), falsely depicted the supratemporal as not only separating widely the parietal and tabular, but also the postparietal and tabular. This error was revealed not only by examination of the *D. absitus* skulls, but the skull of the small, juvenile, holotypic skeleton of *D. sanmiquelensis* (MCZ 2989) described by Lewis and Vaughn (1965) from the Early Permian Cutler Formation of Colorado (not available until this study). The temporal region in the North American *Diadectes* is reinterpreted here as identical to that in the German specimens. This revision, however, does not alter the analysis of the interrelationships of the diadectomorphs presented by Berman et al. (1992).

There are also several features of the postaxial presacral vertebrae of *D. absitus* that may appear to differentiate it from North American species. These differences are most likely the result of proportional growth changes, as almost all the illustrations and descriptions of North American species are based on much larger and, therefore, undoubtedly more fully mature specimens than those known from Germany. The most noticeable among these differences include: 1) in *D. absitus* the neural spines are much lower; 2) the crests of the posterior zygapophyseal buttresses occupy a nearly horizontal plane in *D. absitus*, whereas in North American species the buttresses slope ventrally at about a 25° angle from the horizontal;

and 3) hypantrum and hyposphene accessory articulations are, as far as can be determined, absent in *D. absitus*. That the above vertebral features of *D. absitus* may reflect an early adult stage of growth is suggested by their occurrence in a comparably sized juvenile or subadult specimen of *Diadectes* (CM 38036) from the Lower Permian (Wolfcampian) Cutler Formation of north-central New Mexico. Using the greatest transverse width of the presacral vertebrae (distance between ends of the posterior zygapophyses) as a means of comparison, the 5-cm measurement of the North American specimen is approximately only one centimeter narrower than those in the German specimens MNG 8853 and 7721. The North American specimen (CM 38036), however, possesses one prominent feature of the presacral column not seen in the German specimens, the alternation in height and structure of the neural spines (Sumida, 1990). This feature is common among late Paleozoic tetrapods, but in at least one form, the large captorhinid *Labidosaurus*, both morphotypes occur (Sumida, 1987, 1990). It was suggested (Sumida, 1987) that the variability of this feature in this genus might represent either a sexual dimorphic or a specific difference.

New Autapomorphies of Diadectes

In the course of describing the Bromacker *Diadectes* two additional cranial autapomorphies of this genus have been identified in addition to those recognized by Berman et al. (1992) that appear to set it apart from other diadectomorphs: 1) the palatal ramus of the pterygoid not only makes a substantial contribution to the posterior medial border of the internal naris, but also prevents a palatine–vomer contact; and 2) the supratemporal has a broad contact with the dorsal margin of the paroccipital process of the opisthotic of the braincase. Inadequate materials prevent determining the presence or absence of the above autapomorphies in the very closely related, nearly identical Late Pennsylvanian *Desmatodon*. These autapomorphies further strengthen the conclusion of Berman et al. (1992) that the highly derived nature of the genus *Diadectes* makes it the least desirable member of the diadectomorphs as a potential outgroup in phylogenetic analyses of the interrelationships of amniotes.

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